

RECRUITMENT PATTERNS AND PROCESSES IN CANADIAN PARKLAND MALLARDS

A Thesis Submitted to the College of
Graduate Studies and Research
In Partial Fulfillment of the Requirements
For the Degree of Doctor of Philosophy
In the Department of Biology
University of Saskatchewan
Saskatoon

By

Daniel W. Coulton

PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a postgraduate degree from the University of Saskatchewan, I agree that the libraries of this university may make it freely available for inspection. I further agree that permission for copying of this thesis in any manner, in whole or in part, for scholarly purposes may be granted by the professors who supervised my thesis work or, in their absence, by the Head of the Department of Biology or the Dean of the College of Arts and Science in which my thesis work was done. It is understood that any copying or publication or use of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis.

Requests for permission to copy or to make other use of material in this thesis in whole or in part should be addressed to:

Head of the Department of Biology
University of Saskatchewan
Saskatoon, Saskatchewan
S7N 5E2

Recommended citation:

Coulton, D. W. 2008. Recruitment patterns and processes in Canadian parkland mallards. Ph.D. thesis, University of Saskatchewan, Saskatoon, Canada.

ACKNOWLEDGEMENTS

My graduate experience has been filled with interesting challenges and people that I will appreciate forever; numerous people have contributed in varying capacities which permitted completion of this thesis. I would like to begin by thanking Dr. John Eadie for agreeing to serve as my external examiner, and for his insight and thought provoking and challenging questions. I thank my graduate advisory committee members, Drs. Ken Belcher, Keith Hobson, and Francois Messier for their constructive criticism and advice on how to improve my research. I was fortunate to have office space at the Canadian Wildlife Service, which provided me the opportunity to interact daily with a group of students and staff with whom I share many professional and personal interests. I am grateful to all the people who worked so hard to help me collect the data for this project including Hollie Remenda, Steve Leach, Jason Estrella, Curt Francis, Jake Groth, Shannon Haszard, David Johns, Glenn Mack, Julie Mackey, Carly Michie, Letty Reichart, Brian Sauer, Josh Traylor, and Lindsay Ware. There have also been numerous and anonymous contractors, volunteers, and employees of the U.S. Fish and Wildlife Service, Canadian Wildlife Service, and Ducks Unlimited who are also appreciated for their help with data collection efforts. I thank Josh Traylor and Gustaf Samelius for great discussions in the nerve centre. In particular, I owe a lot of gratitude to Kevin Dufour for tolerating my interruptions for statistical advice and discussion, comments on manuscript drafts, for great bar-b-q, and just being a good friend.

I am grateful for the financial support I received from the following organizations: Delta Waterfowl Foundation, Institute for Wetland and Waterfowl Research (Ducks Unlimited Canada), Environment Canada, Natural Science and Engineering Research Council (via grant to Bob Clark), and the University of Saskatchewan, and for logistical and in-kind support from Delta Waterfowl Foundation, Institute for Wetlands and Waterfowl Research, U.S. Fish and Wildlife Service, and Canadian Wildlife Service.

I would especially like to thank my supervisors Drs. Bob Clark and Serge Larivière for believing in me and providing me the opportunity to pursue my ambitions, for creating a good learning environment, and friendship. I am grateful to the Haszard

and Coulton clans for their encouragement and continued support throughout graduate education. Last, I acknowledge the sacrifice, support, and patience of my wife Shannon Haszard; thank you for being there for me.

GENERAL ABSTRACT

An improved ability to assess whether individuals have been added through immigration or natality and lost through emigration or mortality could alleviate several problems in population ecology. Fortunately, advances in stable isotope techniques now allow the movements of individuals to be retraced from tissue values and provide an opportunity to link information about the origins of individuals with demographic rates so that questions about the significance of dispersal can be assessed. I used such an approach by combining feather isotope information with demographic rates derived from capture-mark-recapture of individual mallards (*Anas platyrhynchos*) breeding in the Canadian aspen parklands, at multiple spatiotemporal scales, to answer questions about population persistence, settling patterns by dispersers, and the fitness of immigrant birds relative to residents.

Feather isotope ($\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$) values from an independent sample of flightless mallard ducklings sampled from across the mid-continent breeding range was used to validate an existing model used for origin assignments. Spatial resolution analysis within the mid-continent mallard breeding range generally showed a loss in prediction when attempting to assign individuals to more narrowly separated geographic origins among boreal, aspen parkland and prairie regions. For feather δD , spatial resolution may be limited by temporal patterns of local climatic events that produce variability in consumer tissue values. Thus, the use of multiple feather isotope signals would provide more reliable information about the origin of individuals for addressing questions about long-distance dispersal in yearling mallards.

Demographic rescue in an apparent population “sink” near Minnedosa, Manitoba, Canada, was due to elevated survival rates from a highly productive group of nesting female mallards using nest tunnels (i.e., an artificial nesting structure) and recruitment of yearling females having natal origins within the aspen parklands. There was little evidence that immigration by yearling females dispersing long-distances was important to annual population growth rates. Consistently high annual survival rates of adult females using nest tunnels lowered the recruitment rates needed for population stability. While tunnel-origin and within-region recruitment of yearling females were nearly equally important to local population growth rate, fine-scale limitations of

isotopic origin assignments prevented further assessment of where recruits originated from within the aspen parkland region.

Factors related to breeding area settling patterns of yearling females are not well understood despite implications to local population dynamics. The likelihood that immigrant yearling females would settle in a parkland breeding area was positively correlated with local breeding-pair density and the amount of perennial nest cover, but was negatively correlated with the amount of wetlands. Although these relationships were not well estimated, they are most consistent a hypothesis that females were attracted to breeding sites by conspecific cues rather than avoidance. Immigrants comprised an average of 9% (range: 0 – 39% over 22 sites) of yearling recruits; most had natal origins in the U.S. prairie pothole region but a non-trivial number originated from the boreal forest, indicating a high degree of connectedness among breeding regions resulting from long-distance natal dispersal.

One of the most frequent explanations for strong site fidelity in breeding female ducks is that females benefit from site familiarity. However, evidence for differential reproductive success between immigrant and resident yearling females was weak. On sites with favourable wetland conditions and low breeding-pair densities immigrant females were more likely to breed and nest successfully than were residents whereas under opposite wetland and pair conditions, resident females were favoured. Thus, the costs and benefits of a natal dispersal decision seemed to vary with social context and environmental conditions, and further work is needed to clarify these processes.

TABLE OF CONTENTS

PERMISSION TO USE	i
ACKNOWLEDGEMENTS.....	ii
GENERAL ABSTRACT	iv
CHAPTER 1. RECRUITMENT AND POPULATION DYNAMICS: A GENERAL INTRODUCTION.....	1
1.1 POPULATION DYNAMICS	1
1.2 PATTERNS OF RECRUITMENT IN DUCKS.....	3
ORAGANIZATION OF THESIS.....	6
CHAPTER 2. NATAL ORIGIN OF YEARLING FEMALE MALLARDS AS DETERMINED BY FEATHER $\delta^{34}\text{S}$, δD, $\delta^{15}\text{N}$, AND $\delta^{13}\text{C}$ VALUES	7
2.1 ABSTRACT	7
2.2 INTRODUCTION	7
2.4 METHODS	9
2.4.1 <i>Collection of feather isotopic standards</i>	9
2.4.2 <i>Measurement of feather $\delta^{34}\text{S}$, δD, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values</i>	11
2.4.3 <i>Data analysis</i>	11
2.4 RESULTS	14
2.4.1 <i>Model validation</i>	14
2.4.2 <i>Spatial resolution</i>	17
2.5 DISCUSSION	20
2.5.1 <i>Reliability of assignments</i>	20
2.5.2 <i>Spatial resolution of assignments</i>	22
CHAPTER 3 SOURCES OF YEARLING FEMALE RECRUITS IN AN APPARENT “SINK” POPULATION	25
3.1 ABSTRACT	25
3.2 INTRODUCTION	25
3.3 METHODS	30
3.3.1 <i>Study area</i>	30
3.3.2 <i>Data collection</i>	30
3.3.3 <i>Yearling natal-origin assignment</i>	31
3.3.4 <i>Capture-recapture analysis</i>	32
3.4 RESULTS	36
3.4.1 <i>Recaptures of marked females</i>	36
3.4.2 <i>Yearling natal-origin assignments</i>	36
3.4.3 <i>Model assumptions</i>	37
3.4.4 <i>Model selection</i>	39
3.4.5 <i>Population growth, apparent survival, and capture</i>	41
3.5 DISCUSSION	41
3.5.1 <i>Sources of population rescue</i>	41
CHAPTER 4. SOCIAL AND HABITAT CORRELATES OF YEARLING MALLARD IMMIGRATION IN THE CANADIAN PARKLANDS.....	45
4.2 INTRODUCTION	45
4.3 METHODS	48

4.4 RESULTS	51
4.4.1 <i>Yearling regional-origin assignments</i>	51
4.4.2 <i>Model selection</i>	52
4.5 DISCUSSION	53
4.5.1 <i>Correlates of immigration</i>	53
4.5.2 <i>Movements among biomes</i>	56
CHAPTER 5. CONSEQUENCES OF NATAL DISPERSAL IN YEARLING FEMALE MALLARDS: A TEST OF THE SITE FAMILIARITY HYPOTHESIS	58
5.1 ABSTRACT	58
5.2 INTRODUCTION	59
5.3 METHODS	62
5.4 RESULTS	64
5.4.1 <i>Natal origin assignments</i>	64
5.4.2 <i>Model selection</i>	65
5.4.3 <i>Fitness components</i>	67
5.5 DISCUSSION	68
5.5.1 <i>Variation in fitness components</i>	68
5.5.2 <i>Variation in breeding probability</i>	73
APPENDIX A. BROAD AND LOCAL-SCALE PATTERNS OF TEMPORAL VARIATION IN FEATHER DEUTERIUM VALUES OF WATERBIRDS	101
A1.1 ABSTRACT	101
A1.2 INTRODUCTION	102
A1.3 METHODS	106
A1.4 RESULTS	111
A1.4.1 <i>Variance components at broad and local scales</i>	111
A1.4.2 <i>Temporal patterns at a parkland site</i>	113
A1.5 DISCUSSION	116
A1.5.1 <i>Sources of temporal variation at a single site</i>	119

LIST OF TABLES

Table 2.1. Misclassification matrices of known-origin mallard feathers sampled at central prairie and northern Canada locations in the mid-continent breeding range during 2005.....	15
Table 2.2. Global cross-validation matrices of mallard feather origin predictions at spatial resolutions of 1, 2, 3, 4, and 5° relative latitude separation of mid-continent boreal forest (BOR) and prairie (PRA) from Canadian aspen parkland (PARK) sites..	18
Table 3.1. Mallard breeding-pair and wetland densities (km^2) and nest success (%NS) (km^2) estimates near Minnedosa, Manitoba, Canada. Some variables were not reported (NR) by references.	29
Table 3.2. Covariate description and values used to model annual variation in population growth (λ), apparent survival (ϕ), and capture (p) rates for marked mallards at Minnedosa, Manitoba, 2002-2005.....	34
Table 3.4. Model selection results for evaluating sources of demographic rescue of female mallards captured at Minnedosa, Manitoba, Canada, 2002-2005..	40
Table 4.1. Descriptive attributes of sampling locations including year, degree latitude (LAT, ° N) and longitude (LONG, ° W), size (km^2), mallard breeding-pair density (km^2) (PAIRS), percent habitat in wetlands (PONDS) and perennial nesting cover (NCOV), and estimates of yearling recruits from Canadian boreal forest (BOR) and aspen parklands (PARK), and U.S. prairie pothole region (PPR) determined from feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values....	49
Table 4.2. Model selection results for the association of site-specific ratio of immigrant to resident yearling recruits with local breeding-pair density (PAIRS), percent habitat in wetlands (PONDS) and nest cover (NCOV) and intercept (INTERCEPT) either singly in additive (+) or interaction (*) combinations..	52
Table 4.3. Model-averaged regression coefficients (β), standard errors (SE), and cumulative normalized weights (Σw) for social and habitat covariates of the ratio of immigrant to resident recruit at 22 breeding locations in the Canadian aspen parklands, 1993-2000.	53
Table 5.1 Model selection results for hatch rate (A, n = 665) and breeding propensity (B, n = 426) of yearling females monitored at 22 breeding locations in the Canadian aspen parklands during 1993-2000..	66
Table 5.2. Logit scale parameter estimates for yearling female mallard breeding propensity (b_i) and hatch rate (h_i) based on model selection results from Tables 5.1A and B.....	66
Table 5.3. Top five models evaluating hatch rate of yearling female mallards (n = 375) monitored at 15 sites in the Canadian aspen parklands, 1993-2000, relative to residency status..	67
Table A1.2. Variance component estimates (%) from analysis of variance for the random effects of year (YEAR) and fall banding station-YEAR interaction (INT) of variation in δD_f values from flightless mallards sampled within boreal forest (BOREAL), boreal transition (BORT), aspen parkland (PARKLAND), and prairie (PRAIRIE) Canada, 1999-2001 and 2005.	112

Table A1.3. Mean ponds at hatch (P_{hatch}), cumulative precipitation volume (mm) during winter prior to hatch (CP_{wint}) and current growing-season (CP_{cgs}), and deuterium values (‰) in amount-weighted growing-season rainfall (δD_p) and yearling mallard feathers (δD_f) during 1994-1998 at St. Denis National Wildlife Area, Saskatchewan, Canada..	115
Table A1.4. Top five candidate models evaluating sources variation in yearling mallard feather deuterium values at St. Denis Wildlife Area, St. Denis, Saskatchewan, Canada, during 1995-1998..	115
Table A1.5. Annual mean (SD, n) δD_f values (‰) from flightless mallards captured at fall banding stations in the boreal forest (BOREAL), boreal transition (BORT), aspen parklands, (PARKLAND), and prairies (PRAIRIE) of western Canada..	117

LIST OF FIGURES

Figure 2.1. Distribution of mid-continent mallard feather sampling sites during 1999-2001 (Hebert and Wassenaar 2005a) (black triangles) and in 2005 (open circles).	10
Figure 2.2. Mean (\pm 95% CI) mallard feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values for Alaska (ALASKA), California (CAL), central prairie (CPRAIRIE), and northern Canada (NORTH) sampled in 1999-2001 (Hebert and Wassenaar 2005a) (black) and during 2005 (grey).	16
Figure 2.3. Mean $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values (‰) (\pm 95% CI) of mallard feathers grown in boreal, aspen parkland, and prairie ecoregions during 1999-2001 and 2005.	19
Figure 3.1. Model-averaged estimates (\pm 95% CI) of annual population growth rate (λ_i) for tunnel (A) and non-tunnel nesting (B) female mallards at Minnedosa, Manitoba, Canada, for 2002-2003, 2003-2004 and 2004-2005.	38
Fig. 5.1. The relationship between hatch rates of yearling female mallards and breeding-pair density (km^2) relative to 25 th (black line), 50 th (dotted line), and 75 th (gray line) quartiles of wetland abundance across 22 locations (circles) in the Canadian aspen parklands, 1993-2000.	69
Figure 5.2. (A) Probability estimates (\pm SE) of hatch rate (h_i) and (B) breeding propensity (b_i) relative to breeding pair density (km^2) for yearling female mallards estimated to be immigrants (open circle, $n = 33$) or residents (closed circle, $n = 200$) at breeding locations in the Canadian aspen parklands during 1993-2000.	71
Figure 5.3. Model-averaged hatch probability estimates (\pm SE) versus breeding pair densities at different levels of wetland density for immigrant (open circles, $n = 47$) and resident (closed circles, $n = 328$) yearling female mallards at breeding locations in the Canadian aspen parklands, 1993-2000.	76
Figure A1.1. Mean (\pm SD) monthly precipitation deuterium values (δD_p) during 1990-2005 (A) and (B) monthly precipitation deuterium values (δD_p) during 1994 (open circle), 1995 (closed circle), 1996 (open triangle), 1997 (closed triangle), and 1998 (open square) at St. Denis Wildlife Area, St. Denis, Saskatchewan, Canada.	104
Figure A1.2. Sampling locations of mallard feathers during fall banding (1999-2001, and 2005) and during the breeding-season at St. Denis National Wildlife Area (1994-1998), Saskatchewan and Minnedosa, Manitoba (2002-2005).	107
Figure A1.3. Sizes and distribution of wetlands during June, 2007 at St. Denis National Wildlife Area, St. Denis, Saskatchewan, Canada.	108
Figure A1.4. Annual distributions of deuterium values from yearling mallard female feathers (δD_f) grown at St. Denis Wildlife Area, St. Denis, Saskatchewan, Canada during 1994-1998. Shown are median (horizontal line within shaded box), 25 th percentile (box boundary nearest zero), 75 th percentile (box boundary farthest from 0), the 10 th and 90 th percentiles (horizontal lines), and extreme values (closed circles).	114
Figure A1.5. Expected mean (\pm 95%CI) deuterium values (‰) of feathers (δD_f , closed circles) versus amount-weighted precipitation for a period extending	

from the <i>prior</i> growing-season (i.e., about 15 months earlier) through the end of feather synthesis (δD_{pgs}) for yearling female mallards at St. Denis National Wildlife Area, Saskatchewan, Canada, during 1995-1998..	120
Figure A1.6. Annual values of deuterium in feathers (D_f) and current growing-season precipitation (D_{cgs}) of female mallards at St. Denis National Wildlife Area, Saskatchewan, Canada, during 1994 (open circle), 1995 (closed circle), 1996 (open triangle), 1997 (closed triangle), and 1998 (open square).....	122

CHAPTER 1. RECRUITMENT AND POPULATION DYNAMICS: A GENERAL INTRODUCTION

Few animal populations remain constant from year to year, and annual population fluctuations at local, regional or larger scales may be produced either by spatiotemporal changes in survival and reproductive rates or by movements of individuals.

Understanding causes of population changes remains a key challenge in ecology and conservation, and is the central theme for my thesis.

1.1 POPULATION DYNAMICS

A population is defined as a group of individuals of the same species occupying the same place at the same time (Krebs 1972). For a species across its entire distribution, population growth rate is a function of birth and death rates over time and changes in environmental conditions may cause birth and death rates to fluctuate. Within this broad distribution there exists a finer scale network of subpopulations linked together by the exchange of individuals responding to habitat variability, inbreeding avoidance, and intraspecific competition (Clobert et al. 2001). The concept that populations are open to exchange of individuals has long been recognized (MacArthur and Wilson 1963) yet the process of dispersal is one of the largest knowledge gaps in population ecology despite its implications to population dynamics and persistence, gene-flow, and evolution of species (Clobert et al. 2001). This deficiency arises largely due to an inability to determine which individuals have been added through local birth or immigration, or removed by death or emigration (Hanski 2001).

Dispersal is related to population growth because individuals from elsewhere may immigrate into populations therefore increase population size whereas others may emigrate and decrease it. Recruitment represents the addition of individuals through either local births or immigration (Williams et al. 2002) and if immigration occurs and is ignored, then inferences about local productivity and population dynamics could be confounded. Additionally, immigrants from far way environments may not be adapted to local conditions and therefore negatively impact local demographic rates. The extent to which this can occur depends on both the demographic rates and the proportion of

immigrant recruits. To fully understand the recruitment process it is necessary to distinguish both local and immigrant recruits and their respective demographic rates.

Advances in capture-mark-recapture (CMR) permit estimation and modeling of demographic and movement rates from marked individuals (Hestbeck et al. 1991, Brownie et al. 1993) but this approach requires the recapture of individuals marked elsewhere and recapture may be problematic when marked populations are separated across great distances. An alternate approach which overcomes this sampling constraint is the use of intrinsic biological markers such as stable isotope values of consumer tissues and it does so because each individual sampled provides information about the origin where tissues were grown. This is possible because values of several naturally occurring stable isotopes vary geographically and are incorporated into tissues of consumers in local food webs (review by Rubenstein and Hobson 2004), and this technique may be reliable if isotopic landscapes are unique. An integrated approach using CMR and tissue isotopic assignments would link demographic rates with information about individual origin across coarse or broad spatial scales and may provide an evaluation of patterns in the recruitment process at local scales.

Previous research in waterfowl has demonstrated that stable sulphur ($\delta^{34}\text{S}$), hydrogen (δD), nitrogen ($\delta^{15}\text{N}$), and carbon ($\delta^{13}\text{C}$) isotopes can be useful as intrinsic origin markers of waterfowl in mid-western North America (Hebert and Wassenaar 2005a) and potentially to the spatial scale of my study. This is because naturally-occurring concentrations of these isotopes vary geographically as a result of abiotic and biotic processes affecting the ratio of heavy to light forms of these elements. Mechanisms causing values of $\delta^{34}\text{S}$ vary spatially include the distribution of light and heavy sulfides in bedrock, anaerobic or aerobic respiration of plants and bacteria present in terrestrial and aquatic systems, and deposition of aerosols from natural or anthropogenic sources (review by Rubenstein and Hobson 2004). Spatial structure emerging from these processes includes more negative $\delta^{34}\text{S}$ values in areas of increasing agriculture activity (Hebert and Wassenaar 2005a) and more positive values in areas close to marine environments. Atmospheric δD enters terrestrial food webs via deposition of meteoric water and values vary geographically due to the influence of local climate on evapotranspiration rates (Craig et al. 1963). This relationship results in

a predictable spatial gradient of more negative values of δD in precipitation occurring with increasing latitude (Hobson and Wassenaar 1997) and altitude (Meehan et al. 2004) in North America and elsewhere in the world (Bowen et al. 2005). Important processes contributing to spatial $\delta^{15}N$ variability include whether plants fix nitrogen symbiotically with microbes or directly from the atmosphere (Marshall et al. 2007). In addition to natural processes, anthropogenic inputs from agricultural fertilizer or livestock manure result in more enriched (positive) $\delta^{15}N$ values than in non-impacted areas (Hobson 1999, Hebert and Wassenaar 2001, Amundson et al. 2003). Variation in terrestrial $\delta^{13}C$ values depend on how carbon from CO_2 is fixed by plants utilizing C_3 , C_4 , or CAM photosynthesis (Kelly 2000). As a result of how these photosynthetic pathways are distributed relative to environmental temperature and aridity, terrestrial $\delta^{13}C$ values tend to be more negative with increasing latitude and more positive with increasing altitude (Wassenaar and Hobson 1998, Suits et al. 2005, Marshall et al. 2007).

The varied of movement patterns, reproductive strategies, and survival rates make avian species ideal for investigating relationships between dispersal and life history traits (Clark et al. 2004). Birds occupying unstable environments may be more inclined to disperse because environments are unpredictable and may require greater search time to locate suitable breeding habitat. North American ducks comprise a group of highly mobile birds whose abundance and reproductive success are linked to spatiotemporally dynamic wetland resources, providing an ideal opportunity to investigate questions about the role of dispersal in population ecology. How dispersing individuals respond to selective pressures relative to non-immigrants in local environments is fundamental to the role of dispersal in population dynamics and the evolution of dispersal behaviour. I combined CMR and isotopic approaches to answer questions related to sources, patterns, and comparative demography of recruits in avian breeding populations occupying unstable environments.

1.2 PATTERNS OF RECRUITMENT IN DUCKS

North American duck populations typically fluctuate annually (Wilkens et al. 2006) in response to changes in demographic rates (Anderson et al. 1992, Hoekman et

al. 2002). Of these variables, recruitment is believed to have the largest influence on population growth rates, and nest success and duckling survival represent the most influential components of annual recruitment rates at broad scales (Cowardin and Blohm 1992, Johnson et al. 1992, Hoekman et al. 2002). To my knowledge relative contribution of immigration to recruitment in local breeding populations has never been measured in waterfowl despite evidence of regional-scale shifts in the annual distribution of ducks relative to habitat conditions (Johnson and Grier 1988).

The primary breeding grounds for most waterfowl are located in the north central United States and Canada, an area composed of prairie and aspen parkland habitat known as the prairie pothole region (PPR; Bellrose 1980, Batt et al. 1989). The reproductive effort of ground nesting duck species has been linked to availability of wetlands (Nichols et al. 1982, Johnson and Grier 1988), the latter being affected most by regional winter and spring precipitation levels, especially in prairie habitats where temporary and seasonal wetlands predominate. Aspen parkland habitats contain more semi-permanent and permanent wetlands and may be more consistent in attracting breeding ducks especially when drought degrades wetland conditions in the southern prairies (Greenwood et al. 1995). When drought conditions prevail across the southern prairies, breeding ducks redistribute themselves into northern aspen parkland and boreal biomes because wetland conditions are more favourable (Johnson and Grier 1988). However, it is generally believed that nest productivity is lowest in boreal habitats, followed by aspen parkland and prairie (Calverley and Boag 1977, Greenwood et al. 1995, Reynolds et al. 2001).

The PPR annually supports large breeding populations of dabbling ducks (*Anas spp.*), especially when wetlands are abundant, but reproductive success generally is sufficiently low that much of the region could be characterized as a “sink” (Pulliam 1988) or ecological trap (Schlaepfer et al. 2002) because habitat appears favourable to fitness but is not. Breeding habitat has been severely degraded by agriculture in much of this region and this has likely increased foraging efficiency of predators and lowered nest success (Greenwood et al. 1995). Local populations which persist despite poor reproductive success could be sustained through demographic rescue by immigrants. However, this hypothesis has not been tested. If this process occurs and involves bird

movements over large areas, this would also suggest a higher degree of connectedness amongst regions of North America than is currently recognized.

In duck species, females are the more philopatric sex (Greenwood and Harvey 1982, Doherty et al. 2002) and dispersal and fidelity (the complement to dispersal) rates are generally related to age and habitat quality (Arnold and Clark 1996, Arnold et al. 2002, Blums et al. 2003). Adult female ducks typically are more breeding-site faithful and yearlings (one-year old individuals) typically have lower rates of fidelity to natal areas (Anderson et al. 1992, Arnold and Clark 1996). In addition to detection problems, lower recapture rates of yearlings on natal sites may be the result of greater dispersal proclivity (Anderson et al. 1992). Reasons for dispersal include habitat loss, resource competition, variability in habitat quality and inbreeding avoidance (Anderson et al. 1992, Dieckmann et al. 1999). Yearling females dispersing in search of apparently “good” breeding habitat may be vulnerable to ecological traps, resulting in poor reproductive and survival consequences (Schlaepfer et al. 2002).

Reproductive effort and nest success vary geographically in the same year and between years (Klett et al. 1988, Greenwood et al. 1995, McKinnon and Duncan 1999). Breeding-season survival in female mallards (*Anas platyrhynchos*) may also vary with age (Reynolds et al. 1995, Dufour and Clark 2002, Devries et al. 2003). The variability in reproductive success and age-related survival may reflect differences associated with benefits of residency status and breeding site-familiarity of yearlings. Benefits of previous residency may include familiarity with locally abundant food resources, protective habitats or close proximity to kin (Anderson et al. 1992). The site-familiarity hypothesis holds that natal fidelity will improve fitness as indicated by higher breeding-season survival and reproductive success rates for resident than non-resident yearling mallards. Examining costs and benefits of natal dispersal and site-familiarity will reveal information about mallard source-sink dynamics across a broad area of the Canadian prairies.

Little is known about the geographic origins of immigrants or how natal dispersal is influenced by spatial variability in habitat quality. Few studies mark young shortly after hatch and so do not account for duckling survival and age-related differences of reproductive effort (Anderson et al. 1992, Dufour and Clark 2002) in

natal fidelity estimates. Because of these challenges, it is difficult to assess relationships between natal origins, environmental factors, survival and reproductive success for resident and non-resident yearlings in local populations. Recent advances in stable isotope methods now allow delineation of the natal origin of individuals across broad geographic areas (Hobson 2002, Hebert and Wassenaar 2005a, Hobson et al. 2006). However, to date the reliability of origin assignments from tissue stable isotope values has not been validated. The objectives of my research were to:

1. Validate the reliability of feather stable isotope assignments using independently sampled known-source standards not included in the construction of assignment models and evaluate the spatial resolution of isotopic assignments (Chapter 2).
2. Examine sources of demographic rescue in an apparent population “sink” (Chapter 3).
3. Evaluate social and habitat correlates of immigration rates from multiple breeding populations across the Canadian aspen parklands (Chapter 4).
4. Test whether natal fidelity results in higher relative fitness under the site-familiarity hypothesis (Chapter 5).

ORGANIZATION OF THESIS

Each data chapter of my thesis was written in the format of an independent manuscript for publication in peer-reviewed journals. There will be some redundancy in the introduction and discussion sections of some chapters and I have made every effort to reduce this redundancy without sacrificing clarity. Although I always took the lead role in acquiring and analyzing data and writing all papers, I also wish to acknowledge the contributions of Drs. Bob Clark, Keith Hobson, Len Wassenaar, Craig Hebert, Dave Howerter, and Mike Anderson in preparing these manuscripts.

CHAPTER 2. NATAL ORIGIN OF YEARLING FEMALE MALLARDS AS DETERMINED BY FEATHER $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, AND $\delta^{13}\text{C}$ VALUES

2.1 ABSTRACT

The reliability of feather $\delta^{34}\text{S}$, δD , $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to predict individual origin was tested using independently sampled known-origin feather values obtained from the mid-continent mallard (*Anas platyrhynchos*) breeding range during late summer 2005 ($n = 70$). An existing regression tree model developed from mallard feathers from Alaska, California, central prairie and northern Canada averaged 56% correct classification of known-origin test cases. A new tree model, accounting for lack of population exchange over the continental divide, correctly predicted 81% of cases, thus validating the multiple stable isotope approach at broad spatial scales. Spatial resolution analysis within the mid-continent mallard breeding range generally showed a loss in prediction when attempting to assign individuals to more narrowly separated geographic origins among boreal, aspen parkland and prairie regions. Predictive accuracy from global cross-validation averaged from 76-91% among five spatial resolution intervals. Misclassification was attributed to site-specific environmental factors causing feather stable isotope signatures to deviate from regional norms but could also be related to temporal factors. The validation and spatial resolution results support the utility of the feather multiple stable isotope approach for reliable individual origin-assignment at broad and coarse geographic scales.

2.2 INTRODUCTION

The movement of individual birds and connectivity of bird populations are of considerable interest to biologists and wildlife managers for understanding population ecology and developing effective conservation strategies. Additionally, dispersal has important implications for gene flow and disease transmission in birds (Webster et al. 2002). Yet for many migratory bird species, where and why individuals disperse remains poorly understood because of problems with discerning the origin of unmarked individuals.

Traditional methods for studying dispersal in birds include retracing movements by individuals with bands or radio-telemetry. These techniques can be expensive and prone to small sample sizes resulting from technical failures and poor detection following initial capture (Clark et al. 2004). Alternatively, the use of intrinsic markers, such as tissue stable isotope values, can provide useful information about the origin of every individual captured when the composition and physiology of the tissue sampled is known. Thus, the tissue stable isotope approach has the potential to resolve sampling problems associated with banding and telemetry studies because it provides a direct link between capture location and where specific tissues were grown and may be especially useful for individuals dispersing long distances.

Naturally-occurring stable sulfur ($\delta^{34}\text{S}$), hydrogen (δD), nitrogen ($\delta^{15}\text{N}$), and carbon ($\delta^{13}\text{C}$) isotope values vary geographically due to regional patterns in evapotranspiration, geology, ammonification and anthropogenic inputs of nitrogen, as well as plant photosynthetic pathways and water-use efficiency (review by Rubenstein and Hobson 2004, Hebert and Wassenaar 2005a). Individuals incorporate isotopic signatures of the local food web into growing tissues as consumers and for inert tissues, such as feathers, no new isotopic assimilation occurs after the completion of tissue synthesis. Thus, tissue isotopic values will be available for sampling elsewhere until re-grown. Patterns of molt have been described for a variety of bird species allowing investigators to link where specific feather tracts were grown to different parts of the annual life-cycle. Values of $\delta^{34}\text{S}$, δD , $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feathers could reliably indicate general origin of unmarked birds if isotopic landscapes differ among regions or origins of interest when captured elsewhere.

Recent research in this area indicates that feather $\delta^{34}\text{S}$, δD , $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can provide reliable information about the source of individuals across broad spatial scales in North America (Hebert and Wassenaar 2005a). However, model estimates were validated using stable isotope values from a sub-sample of individuals originating from the same sites and years as used to build the model. This approach causes assignment success to be biased high because the same information used to create the model is used to validate it. A more rigorous evaluation includes validating with samples not used during model building. This type of model validation will identify

how robust individual level isotope-based origin-assignments are to variability not incorporated into estimation. The primary objective of my study was to validate the multiple stable isotope approach for discerning geographic origin. My secondary objective was to examine how varying spatial separation among regions of origin influences classification accuracy.

2.4 METHODS

2.4.1 *Collection of feather isotopic standards*

Greater-secondary covert feathers (GSC) were sampled from 70 pre-fledged mallard young during July-August 2005 at 13 waterfowl banding stations (sites) across the mid-continent mallard breeding range (Fig. 2.1). Feathers were collected from 3 sites located in the Northwest Territories (n = 10), and 10 sites in the Canadian (4 Alberta, 1 Saskatchewan, 2 Manitoba; n = 43) and U.S. prairies (2 North Dakota, 1 South Dakota; n = 17). Feathers were sampled from flightless young; thus, stable $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values of feather tissue should reflect the isotopic values of the local food web since these feathers could not have been grown elsewhere.

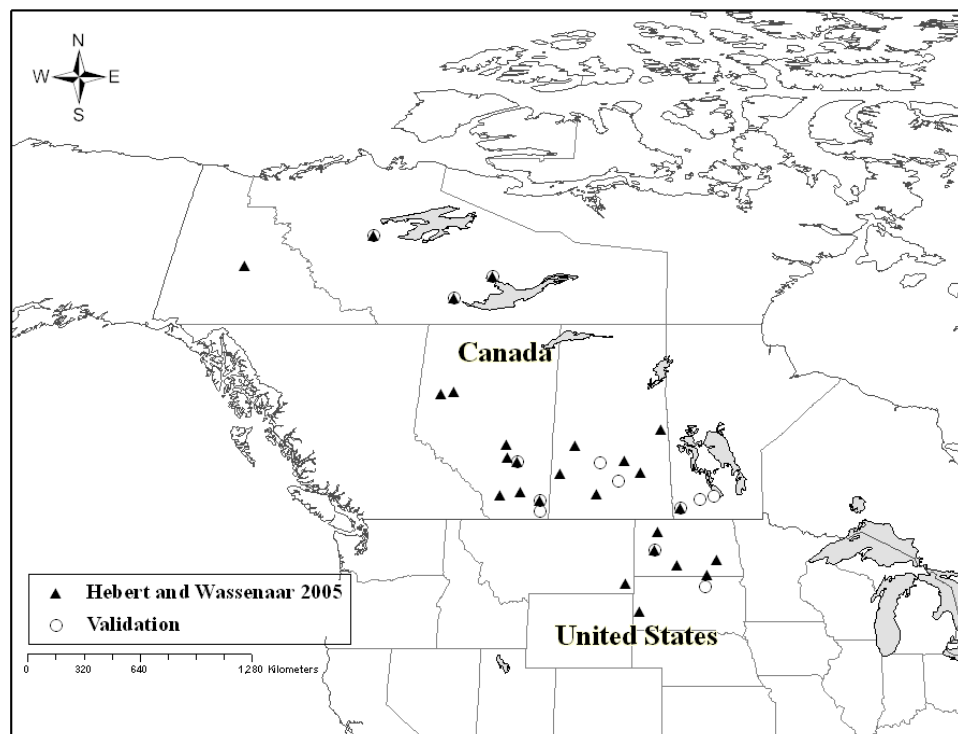


Figure 2.1. Distribution of mid-continent mallard feather sampling sites during 1999-2001 (Hebert and Wassenaar 2005a) (black triangles) and in 2005 (open circles).

GSC were also sampled from females marked as ducklings and then recaptured as yearlings during 1986-2000 at St. Denis, Saskatchewan, Canada, and during 2002-2005 at Minnedosa, Manitoba, Canada, providing additional known-age and origin δD , $\delta^{15}N$, and $\delta^{13}C$ feather values but not $\delta^{34}S$. These samples reflect local isotopic signatures because yearling female mallards retain GSC grown as ducklings until after their first breeding season as yearlings (Heitmeyer 1987).

2.4.2 *Measurement of feather $\delta^{34}S$, δD , $\delta^{15}N$, and $\delta^{13}C$ values*

Feathers were cleansed in a chloroform and methanol solution (2:1 volume ratio, respectively) and dried in a fume hood for at least 24 hours. A 1.0-1.8 mg sample of feather barbs was used for sulfur, nitrogen, and carbon, and a 350-ug sample for hydrogen isotope analyses. All barb material was taken from the base of feathers to represent the most recently grown tissue. Samples were combusted using pyrolytic continuous-flow isotope-ratio mass spectrometry (CFIRMS) to determine sulfur ($^{34}S/^{32}S$), nitrogen ($^{15}N/^{14}N$), and carbon ($^{13}C/^{12}C$) isotope ratios. Deuterium ratio ($^2H/H$) values of non-exchangeable feather hydrogen were determined using on-line high temperature flash pyrolysis and with normalization equations from keratin standards (Wassenaar and Hobson 2000, Wassenaar and Hobson 2003). All stable isotope ratio results are reported in delta notation (δ), in units of per mil (‰), and normalized to respective international standards (hydrogen: Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation Scale), (carbon: Pee Dee Belemnite), (nitrogen: air), and (sulfur: Canyon Diablo Triolite). Measurement error was $\pm 0.5\text{‰}$, $\pm 2.0\text{‰}$, $\pm 0.2\text{‰}$, and $\pm 0.1\text{‰}$, and for $\delta^{34}S$, δD , $\delta^{15}N$ and $\delta^{13}C$, respectively. Sulfur analysis was conducted at the University of Waterloo, Waterloo, Ontario, Canada. Analysis for hydrogen was conducted at the National Water Research Institute, Saskatoon, Saskatchewan, Canada. Feather nitrogen and carbon were analyzed at the University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

2.4.3 *Data analysis*

Hebert and Wassenaar (2005a) developed an origin-assignment classification tree based on individual mallard feather $\delta^{34}S$, δD , $\delta^{15}N$, and $\delta^{13}C$ values of known-

origin ($n = 230$). Their model was developed using discriminant-based univariate splits of these stable isotope values for geographic regions of Alaska, California, northern Canada, and central prairies. To test the reliability of their classification model, I assigned individual feathers to the same broad geographic origin groups including northern Canada (Yukon and Northwest Territories, $n = 10$) and central prairies (Alberta, Saskatchewan, Manitoba, North Dakota, and South Dakota, $n = 60$) but I did not have samples from either Alaska or California. I used the same classification tree software and analytical configuration to estimate the origin of known-origin individual feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values for validation. Cross-tabulation of known versus estimated origin of test cases was used to evaluate classification performance. Site-level misclassification was estimated for sites that were sampled in Hebert and Wassenaar (2005a) (same, $n = 8$) to identify the contribution of temporal variability to classification error. A site was considered misclassified if ≥ 1 individual was incorrectly predicted to its known origin. I examined differences in mean $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ feather values among test and model (i.e., Hebert and Wassenaar 2005a) data ($n = 253$) using multivariate analysis of variance (MANOVA) and then considered univariate mean values ($\pm 95\%$ CI) to identify sources of classification error.

Mark-recapture information suggests low mixing of female mallards between Pacific and mid-continent populations (Reinecker 1990). This indicates that flyway capture location provides prior information about likely origins of unknown source individuals. Therefore, I constructed a new classification tree using the same analytical configuration with only Hebert and Wassenaar's (2005a) northern Canada and central prairie $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ feather values ($n = 183$). I believe this approach would reflect a more relevant test of model reliability by eliminating potential sources of estimation error that biologically are unlikely to occur in mid-continent mallards. Cross-tabulation of known versus estimated origin of test cases was then used to evaluate classification success.

To examine the role of regional spatial resolution on isotopic origin-assignment accuracy, I used classification tree analysis with discriminant-based univariate splits (StatSoft 2000). Classification tree analysis used algorithms to perform discriminant-based splits following QUEST (Quick, Unbiased, Efficient Statistical Trees; Loh and

Shih 1997). To avoid over-fitting, classification trees were pruned using a minimal deviance complexity cross-validation (Breiman et al. 1984, StatSoft 2000). This resulted in a classification tree with a minimal number of splits and optimal predictive accuracy. Categorical response variables comprised boreal forest (BOREAL), Canadian aspen parkland (PARKLAND) and prairie (PRAIRIE) ecoregions within the mid-continent mallard breeding range. I used mid-continent feather isotope values from Hebert and Wassenaar (2005a) (n = 183), this validation study (n = 70) with those sampled at St. Denis (n = 67) and Minnedosa (n = 34) as independent predictor variables. Observed ecoregion of feather origin was assigned by GIS overlay of sampling location latitude (LAT) and longitude (LONG) coordinates with a geo-referenced ecoregion map (Ecological Stratification Working Group 1995). Sampling locations identified as boreal transition within the ecoregion map were coded as PARKLAND because the presence of agriculture likely makes this landscape isotopically similar to PARKLAND.

Separate classification tree analyses were conducted representing spatial resolutions of 1, 2, 3, 4, and 5° relative LAT differences of BOREAL and PRAIRIE from PARKLAND. For each analysis, all feather values from PARKLAND were retained (n = 133). I included individual feathers as BOREAL and PRAIRIE dependent on whether sites met minimum resolution criteria using their LAT and LONG coordinates relative to those of PARKLAND sites. Feathers from sites that were less than the minimum LAT resolution criteria from PARKLAND were excluded from each analysis. Thus, sample sizes of BOREAL and PRAIRIE feathers tended to increase as LAT distance from PARKLAND sites decreased.

The predictive accuracy at each spatial resolution was assessed using global cross-validation, where each distance-specific analysis was replicated three times and tested with a hold-out group comprising one-third of the learning sample. I report mean (\pm SD) correct classification rates of the three global cross-validation replicates for each resolution interval analysis. I compared the relative increase in correct classification between each spatial resolution to determine the optimal trade-off between spatial proximity and predictive performance. Finally, I evaluated differences in BOREAL, PARKLAND, and PRAIRIE feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values (n = 253) with

MANOVA and then used mean values (\pm 95% CI) from all four data sources ($n = 354$) to describe regional univariate patterns and sources of classification error.

2.4 RESULTS

2.4.1 *Model validation*

The validation test of Hebert and Wassenaar's (2005a) classification tree model correctly predicted 56% (39 of 70) of known-origin individuals sampled during 2005 (Table 2.1). Incorrect predictions included 24 and 6 individuals originating from the central prairies to California and Alaska, respectively. A single individual from northern Canada was incorrectly predicted to Alaska. The subsequent test of a classification tree developed from only mid-continent feather values correctly classified 81% (57 of 70) of individual cases to northern Canada and central prairie regions. Misclassification occurred in feathers of 13 central prairie birds to northern Canada and no feathers from northern Canada were incorrectly predicted to central prairies (Table 2.1). Site-level misclassification was 0.38 (3 of 8) for those sites which were sampled both in 2005 and during Hebert and Wassenaar (2005a). Classification tree analysis indicated that explanatory variable importance rankings (0-100 scale with 100 being most important) were highest for $\delta^{34}\text{S}$ (100) followed by $\delta^{15}\text{N}$ (32), δD (28) and $\delta^{13}\text{C}$ (20) excluding Alaska and California values.

Multivariate analyses indicated feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values differed for northern (MANOVA, Wilk's Lambda, $F_{4,39} = 3.52$, $P < 0.015$) and central prairie (MANOVA, Wilk's Lambda, $F_{4,204} = 12.21$, $P < 0.001$) regions among validation and model data. Univariate level comparison indicated these differences were related to regional variation in $\delta^{15}\text{N}$ for northern and in $\delta^{34}\text{S}$, δD , and $\delta^{15}\text{N}$ for central prairie regions based on 95% confidence intervals (Fig. 2.2).

Table 2.1. Misclassification matrices of known-origin mallard feathers sampled at central prairie and northern Canada locations in the mid-continent breeding range during 2005 (n =70). Regional origin was estimated using feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values in an existing classification tree (Hebert and Wassenaar 2005a) (HW) and a new tree developed with only mid-continent values (MC) from 1999-2001.

Estimated-origin	Known-origin					
	HW				MC	
	Alaska	California	central Prairie	northern Canada	central Prairie	northern Canada
Alaska	0	0	6	1	-	-
California	0	0	24	0	-	-
central Prairie	0	0	30	0	47	0
northern Canada	0	0	0	9	13	10
% Correct	-	-	50.0	90.0	78.3	100.0

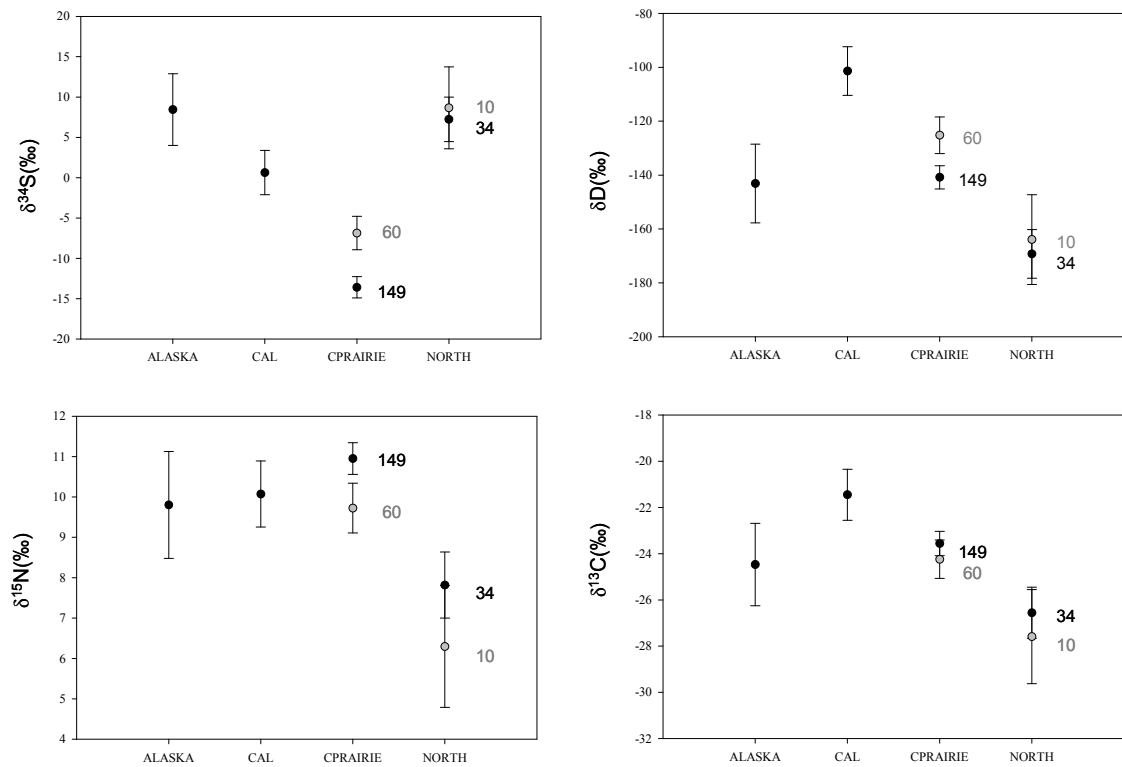


Figure 2.2. Mean (\pm 95% CI) mallard feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values for Alaska (ALASKA), California (CAL), central prairie (CPRAIRIE), and northern Canada (NORTH) sampled in 1999-2001 (Hebert and Wassenaar 2005a) (black) and during 2005 (grey). Sample sizes listed to right of data points.

2.4.2 *Spatial resolution*

Percent average classification success (\pm SD) from global cross-validation was 79.0 (2.5), 76.0 (2.4), 78.9 (3.4), 89.1 (3.4), and 90.7 (3.3) for relative 1, 2, 3, 4, and 5° LAT resolution intervals, respectively. The best predictive performance and closest spatial proximity occurred when region-specific sampling locations were separated by at least 4° relative LAT. At this resolution, isotopic assignment was 2.7 times better than by chance after accounting for priors. Region-specific predictive accuracy varied among distance intervals but was generally lowest for PARKLAND followed by PRAIRIE and BOREAL (Table 2.2). Most misclassification occurred in individuals originating from PARKLAND being classified as PRAIRIE and vice versa regardless of distance interval. On average, feathers from PARKLAND and PRAIRIE were equally likely to be incorrectly predicted to PRAIRIE and PARKLAND, respectively.

Multivariate analyses indicated that BOREAL, PARKLAND, and PRAIRIE differed in feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values (MANOVA, Wilk's Lambda $F_{8,494} = 43.52$, $P < 0.001$). Univariate mean feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values derived from all data sources indicate regional differences in all four stable isotopes among BOREAL, PARKLAND, and PRAIRIE based on 95% confidence intervals (Fig. 2.3).

Table 2.2. Global cross-validation matrices of mallard feather origin predictions at spatial resolutions of 1, 2, 3, 4, and 5° relative latitude separation of mid-continent boreal forest (BOR) and prairie (PRA) from Canadian aspen parkland (PARK) sites. Individual origin was predicted using known-origin feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values sampled from these ecoregions during 1999-2001 and 2005.

Estimated origin	Known-origin														
	Spatial resolution to PARK (° relative latitude)														
	1			2			3			4			5		
	BOR	PARK	PRA	BOR	PARK	PRA	BOR	PARK	PRA	BOR	PARK	PRA	BOR	PARK	PRA
BOR	45	5	5	52	6	6	50	7	2	42	2	0	41	3	0
PARK	2	98	11	0	79	14	3	100	7	2	119	3	3	117	1
PRA	8	30	74	3	48	47	2	26	20	0	12	14	0	13	10
% Correct	81.8	73.6	82.2	94.5	59.3	70.1	90.9	75.1	68.9	95.4	89.4	82.3	93.1	87.9	90.9

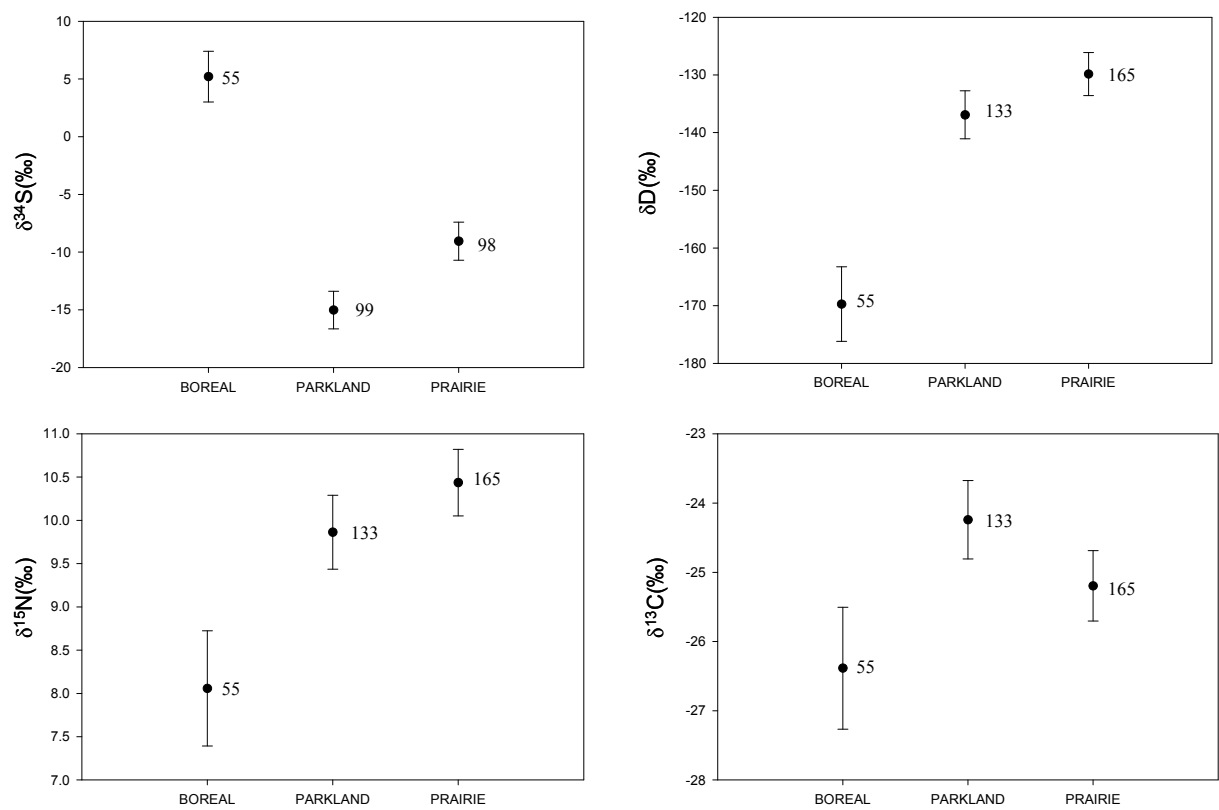


Figure 2.3. Mean $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values (‰) (\pm 95% CI) of mallard feathers grown in boreal, aspen parkland, and prairie ecoregions during 1999-2001 and 2005. Sample sizes at right of mean values.

2.5 DISCUSSION

2.5.1 *Reliability of assignments*

The validation results support previous evidence that $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ feather values can be used to reliably delineate individual origin where tissue was grown (Hobson and Wassenaar 1997, Hebert and Wassenaar 2005a). Overall assignment success of the validation test was 30% lower than global cross-validation results reported by Hebert and Wassenaar (2005a). However, high error rates resulted from misclassification of individuals among Pacific and mid-continent populations. While this validation test suggests this technique performs poorly, the biological relevance of female mallard movements across the continental divide is doubtful based on banding data (Reinecker 1990, Doherty et al. 2002). Thus, a more biologically relevant approach for mallards is to build individual mid-continent and Pacific-flyway models. When mid-continent population was isolated to prevent flyway mixing, correct classification success improved by 25% and was 1.8 times better than by chance relative to prior regional-specific sample sizes. Under this framework, success rates for these two regions are more similar to global cross-validation results reported by Hebert and Wassenaar (2005a) and indicate that predictive performance is high (i.e., 81%) at broad spatial scales using a multi-stable isotope approach.

In addition to non-biologically relevant error, higher misclassification rates of individuals during validation resulted from regional differences in feather $\delta^{34}\text{S}$, δD , and $\delta^{15}\text{N}$ values between data sets (Fig. 2.2). Feathers from the central prairies sampled during 2005 were more enriched in $\delta^{34}\text{S}$ and δD and more depleted in $\delta^{15}\text{N}$ than model data. Feathers grown in agricultural areas are generally more depleted in $\delta^{34}\text{S}$ (more negative $\delta^{34}\text{S}$) and enriched in $\delta^{15}\text{N}$ (more positive $\delta^{15}\text{N}$) (Hebert and Wassenaar 2001, Hebert and Wassenaar 2005a). Differences in central prairie $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values among studies could reflect decreases in the amount of agricultural activity in this region. Given the economic importance of farming to rural communities in the central prairies and the brief time-frame between studies, a large-scale reduction in agricultural activity seems unlikely. It seems more plausible that $\delta^{34}\text{S}$ enrichment and $\delta^{15}\text{N}$ depletion of validation feather values resulted from unbalanced geographical representation of sampling locations between studies. The collection in the current study

included fewer feathers from Saskatchewan and North and South Dakota, areas of generally high agricultural development. A decrease in the feather representation from agricultural areas is consistent with patterns of enrichment and depletion in the central prairie feather $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values, respectively. For feather δD values, temporal variability could arise because of annual changes in seasonal precipitation affecting the loss of δD to atmospheric evaporation or the degree of water body permanence (Hobson and Wassenaar 1997). Continental patterns of growing season precipitation δD values are negatively correlated with latitude and positively correlated with feather δD values (Hobson and Wassenaar 1997, Hebert and Wassenaar 2005a). Thus, annual variation in precipitation rates at sampling locations near the periphery of regional groups could result in similarity of feather δD values among regions and confound predictions. Based on the comparison of site-level misclassification rates, temporal variation contributed to misclassification costs but investigation with a larger sample of sites is warranted.

Among elements studied, $\delta^{34}\text{S}$, δD , and $\delta^{15}\text{N}$ values are important for distinguishing origin of feather tissue at broad spatial scales because of geographical patterns associated with regional geology, climate and anthropogenic activities (Hobson and Wassenaar 1997, Hebert and Wassenaar 2001, Hebert and Wassenaar 2005a). Despite its established utility in other studies, the relatively low importance ranking of δD values for origin assignment during this analysis is not new (Hebert and Wassenaar 2005a). The spatial scaling of this study was restricted to neighbouring northern regional breeding distributions within central North America and so, regional specific differences in δD values are likely less pronounced when origin groups are separated by a smaller distribution of latitudes. However, even across broad-scale latitudes δD may not always be useful such that values can be greater than would be expected based upon latitude alone (Hebert and Wassenaar 2005a). Marked differences in feather $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ among central prairie and northern Canada regions likely reflect the patterns in regional geology that may support or limit cereal-based agriculture and live-stock farming (Hebert and Wassenaar 2001, Hebert and Wassenaar 2005a). Regional patterns in mallard feather $\delta^{34}\text{S}$ values could also mimic the distribution of sulfate-reducing bacteria known to deplete $\delta^{34}\text{S}$ in aquatic food webs (Hebert and Wassenaar 2005a). This study's results suggest feather $\delta^{34}\text{S}$ values alone may have been adequate in

providing reliable predictions for the two mid-continent regions of interest. However, the relative importance of each stable isotope for origin-assignments is likely to vary with the number of assignment groups, the degree of isotopic signature differences among groups, and their spatial arrangement.

2.5.2 *Spatial resolution of assignments*

The results of the spatial resolution analysis indicate that individual origin-assignment using feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values can be highly reliable (>80.0%) at finer spatial scales than previously reported (Hebert and Wassenaar 2005a). Predictive accuracy generally decreased with closer spatial proximity, however, even the lowest accuracy was two times better than by chance. These findings support the utility of feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values as a reliable technique for individual origin assignment.

Correct classification of individuals from aspen parklands and prairies was confounded by isotopic similarity of feather δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values (Fig. 2.3). The resemblance of aspen parkland and prairie isotopic signatures is likely due to common climate, biology, and agricultural development. Enriched feather $\delta^{34}\text{S}$ appears to be a strong segregator of prairie from aspen parkland origins and this pattern may be due to relationships with geology and/or the frequency of aerobic and anaerobic respiration in wetlands (review by Rubenstein and Hobson 2004, Hebert and Wassenaar 2005a). The relative magnitudes of differences in stable isotope values among regions indicate that feather $\delta^{34}\text{S}$ and δD are important for distinguishing boreal forest from aspen parkland and prairie biomes (Fig. 2.3).

Feather $\delta^{34}\text{S}$, δD , and $\delta^{15}\text{N}$ patterns among boreal forest, aspen parkland, and prairie ecoregions during this study are consistent with geographic patterns reported elsewhere (Hobson and Wassenaar 1997, Hebert and Wassenaar 2005a). However, the regional patterns related to feather $\delta^{13}\text{C}$ values deviate from general trends where ^{13}C depletion is positively correlated with increasing latitude (review by Rubenstein and Hobson 2004). Based on this trend, we would have expected aspen parkland feather $\delta^{13}\text{C}$ values to be more depleted (more negative) than prairie but more enriched (more positive) than boreal forest values. Aspen parkland values from samples collected in

2005 included feathers from northern Alberta, which had high ^{13}C enrichment (range: -14.2 to -27.6) given their sampling latitude; a pattern which could be partly caused by higher site elevation (Graves et al. 2002, Hobson et al. 2003) and drier climate than boreal forest at similar latitudes (Hobson 1999).

The validation test of Hebert and Wassenaar's (2005a) feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ model and subsequent spatial resolution analysis support that the stable isotope approach can provide reliable predictions of individual origin at broad and coarse spatial scales. Despite regional variation in feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values, the multi-stable isotope approach to broad-scale origin classification problems appears to be robust when irrelevant sources of error can be removed. This is evident by the 25% increase in classification success when the chance for unnatural exchange of individuals among Pacific and mid-continent mallard populations was excluded from the model. Bayesian techniques can now be used to incorporate sources of error during model building (Wunder and Norris 2008) and provide a better alternative than excluding as done in this study. Regardless, if unnatural exchange of individuals can not be controlled in the development of assignment tests then multiple isotope approach performs poorly.

The application of this technique will provide wildlife managers with the ability to measure connectivity between locations where individuals are sampled and where tissues were grown. However, application of this approach is dependant on chronology of tissue synthesis being known. Geographically linking migratory species across space and time will be useful for identifying important habitats and/or locations for conservation but may also elucidate patterns in population demographics. For example, feathers grown at southern wintering habitats and sampled at northern breeding locations could reveal information related to population mixing (Rubenstein et al. 2002), or rates of fecundity and survival (Norris et al. 2004). Other applications include the delineation of sources of productivity (Hebert and Wassenaar 2005b) and potential applications to wildlife diseases, behaviour, and evolutionary processes (Webster et al. 2002). The accuracy of origin-assignment using the multi-isotope approach was reduced at finer spatial scales but greater resolution may be possible when combined with other tracking techniques such as banding and telemetry (Clark et al. 2004).

Further work is needed to understand how well origin-assignment models developed from one species can be generally applied to others. This might be accomplished by comparing tissue isotopic signatures of different species grown at the same location. If this is possible it would negate the need for building species-specific models. Initial work indicates potential for general applications within waterfowl (Hebert and Wassenaar 2005a) and across species (Clark et al. 2006) but could be impeded by differences in species use of aquatic and terrestrial food webs. These ideas are being explored with models developed from known-origin data from dabbling and diving duck species. The ambition of this work is that it will lead to new insights pertaining to declines in boreal lesser scaup (*Aythya affinis*) and conservation efforts to aid this and other migratory birds.

CHAPTER 3. SOURCES OF YEARLING FEMALE RECRUITS IN AN APPARENT “SINK” POPULATION

3.1 ABSTRACT

Populations occupying “sink” habitats can persist if productive local sub-populations exist, immigrants rescue the population, or both processes occur. I tested these hypotheses by combining capture-mark-recapture data and recruit origin assignments obtained from feather stable isotope values from a local Mallard population breeding near Minnedosa, Manitoba, Canada, during 2002-2005. Important effects to population growth rates included female nest location (nest tunnel versus non-tunnel) and recruitment of yearling females originating locally or from nearby aspen parkland areas rather than from more distant regions. Population growth rates of tunnel-nesting females (mean = 1.21, SD: 0.22, n = 3 years) annually exceeded population stability primarily because apparent annual survival rate was consistently > 0.75 . Population growth rates for non-tunnel females (mean = 0.90, SD: 0.17, n = 3 years) varied annually in response to recruitment rates of yearling females from aspen parkland areas; there was little support for models which represented population rescue by yearling immigrants produced in the United States Prairie Pothole and Canadian Boreal Forest regions. Elevated apparent survival rates of adult females using nest tunnel locations and fine-scale dispersal of yearling females recruited from local subpopulations or nearby source populations are responsible for sustaining local Mallard levels near Minnedosa. This is the first study to demonstrate clearly the value of nest tunnels for increasing adult female survival and productivity of Mallards at a local scale. Integrating mark-recapture and isotopic information may be valuable in testing ecological and management hypotheses about dispersal and demographic processes, as well as determining the value of nest structure programs for avian conservation.

3.2 INTRODUCTION

At least two non-mutually exclusive hypotheses could explain why populations may be stable or growing when local reproductive success is insufficient to offset annual mortality. First, there may be local subpopulations which contribute excess productivity

through either higher survival or reproductive rates, or both. However, the influence of subpopulations will depend on the relative distribution and fitness of individuals in each subpopulation. Alternatively, local populations could be sustained by rescue from immigrants produced elsewhere (Brown and Kodric-Brown 1977), a concept with origins in island biogeography (MacArthur and Wilson 1963). The underlying mechanisms which sustain populations are relevant to source-sink and population dynamics (Pulliam 1988, Watkinson and Sutherland 1995, Boughton 1999), gene flow (Jehle et al. 2005), and conservation (Stacy and Taper 1992).

Modern capture-mark-recapture (CMR) models provide powerful approaches for evaluating components of population growth (Pradel 1996), as well as movement of marked individuals among multiple populations (Hestbeck et al. 1991, Brownie et al. 1993). Recruitment represents new individuals joining a population through either births or immigration (Williams et al. 2002). Linking the origin of recruits to local or external sources is essential for testing the rescue by immigration hypothesis. CMR can quantify movement rates between populations but relies on the recapture of individuals marked elsewhere. For highly mobile species such as migratory birds, recapture rates of banded transients are often <2.0% (see Doherty et al. 2002, Webster et al. 2002), reducing precision of estimates. Alternate CMR methods such as telemetry come with technical, logistical, and financial constraints which may limit sample sizes or spatial representation for making inferences about populations of interest (Clark et al. 2004).

The origin of unmarked individuals can be reliably traced across broad spatial scales using intrinsic biological markers such as tissue stable isotope values (Hebert and Wassenaar 2005a). This is possible because consumers incorporate stable isotopes from local food webs into growing tissues and tissue values can then be compared with geographic patterns (review by Rubenstein and Hobson 2004). For example, molt chronology and sequence have been described for many bird species allowing for the sampling of specific feather tracts to link individual breeding performance to winter habitat use (Marra et al. 1998). The isotopic approach may be especially useful to delineate the geographic sources of unmarked juvenile recruits because metabolically inert tissues such as claws and feathers are often suitable for sampling several months

after young leave natal areas. Thus, the isotopic approach can quantify dispersal and has potential for resolving questions about demographic rescue.

Previous attempts to measure rescue effects in birds used radio telemetry dispersal data in simulated models of population growth (Withey and Marzluff 2005) or telemetry and banding to track individual movements among discrete populations (Martin et al. 2000). CMR and stable isotope analyses were combined, where CMR was used to estimate survival, capture, and population growth rates while tissue stable isotope values were used to infer natal origins of yearling recruits. The combined approach permits the simultaneous consideration of survival and capture rates, with information about sources of recruits and their relative contributions to population growth rate. Adding auxiliary isotopic information is better than CMR alone because each newly captured individual can potentially provide reliable information about its previous location(s). The idea of enhancing CMR with auxiliary stable isotope data has been suggested previously (Webster et al. 2002, Clark et al. 2004, Powell 2004) and used to study fish foraging ecology (Cunjak et al. 2005) and insect patch dynamics (Caudill 2003) but application to real problems in birds are lacking. I provide an example of how CMR and feather stable isotope information can be combined to evaluate hypotheses about local population dynamics in a migratory bird species. I present a temporal symmetry analysis of mark-recapture and feather stable isotope data from a population of adult and yearling female Mallards (*Anas platyrhynchos*) breeding near Minnedosa, Manitoba, Canada, an area where reproduction has typically been too low to sustain the local population.

Artificial nest structures (e.g., baskets, bales and tunnels) for waterfowl have been used in Europe since the 1600s (Eley Game Advisory Station 1969, cited by Doty et al. 1975), were introduced to North America in the 1950s (Burger and Webster 1964), and have been distributed in the Minnedosa area since the early 1990s (J. Fisher, Delta Waterfowl Foundation, pers. comm.). Despite this long history of use, knowledge about the broad demographic impact of nest structures is lacking. Female ducks are most susceptible to predators when attending nests (Sargeant et al. 1984) and over-water nest tunnels may reduce mortality by limiting access by terrestrial predators. Nest tunnels may be practical at improving both nest productivity and female survival because higher

hatch rates result in less renesting, but the female survival hypothesis has not been formally tested. Nests in tunnels, such as nest cylinders, are consistently more productive than those in adjacent upland habitats and other nest structures (i.e., baskets and bales), and it has been hypothesized that tunnels have nest success rates that are sufficient to maintain or increase local populations (Artmann et al. 2001). This hypothesis predicts that annual population growth rates will be influenced largely by previous offspring production such that higher recruitment would result in a local population increase.

There is evidence of low reproductive success for Mallards in many areas of the Canadian prairies (Greenwood et al. 1995), including at Minnedosa, where pair density may be high despite low upland nest success (Table 3.1). Local Mallard populations in these areas could be maintained by immigration from elsewhere. For instance, yearling females may settle more frequently in unfamiliar breeding areas because natal dispersal generally is more common than adult breeding dispersal (Anderson et al. 1992). This hypothesis predicts that annual population growth rate will be positively correlated with yearling immigration rate. The isotopic approach can be applied to female Mallards because greater covert feathers (GSC) grown as ducklings are not molted until after their first breeding season as yearlings (Heitmeyer 1987). Thus, isotopic information related to the natal origin of individuals is available from GSC feathers of yearling females sampled at breeding locations.

Table 3.1. Mallard breeding-pair and wetland densities (km²) and nest success (%NS) (km²) estimates near Minnedosa, Manitoba, Canada. Some variables were not reported (NR) by references.

Year(s)	Pairs	Upland %NS (n)	Tunnel %NS (n)	Wetlands	Reference
2005	7.3	1.9 (24)	74.0 (56)	36.5	Current study
2004	12.6	0.1 (34)	65.5 (68)	31.7	
2003	12.9	2.5 (69)	43.3 (73)	30.2	
2002	16.7	5.7 (96)	51.1 (48)	31.1	
1998	10.4	1.7 (405)	70.9 (72)	50.6	
1985-91	NR	12.2 (49)	NR	NR	IWWR 1999, unpublished Arnold et al. 1993
1984	5.0	10.4 (50)	NR	25.0	Greenwood et al. 1995
1983	8.0	6.3 (54)	NR	44.4	
1971	6.2	5.2 (25)	NR	NR	Sellers 1973
1970	4.6	NR	NR	NR	
1969	4.6	NR	NR	NR	
1955	9.1	29.1 (42) ¹	NR	NR	Dzubin and Gollop 1972
1954	11.3	17.8 (52) ¹	NR	NR	
1953	13.5	19.9 (67) ¹	NR	NR	
1952	14.9	21.0 (52) ¹	NR	NR	

¹ Apparent nest success was transformed to Mayfield equivalent using Green's (1989) estimator.

My general objective was to evaluate the locally productive subpopulation and yearling immigration hypotheses to explain local Mallard population dynamics in a putative sink breeding habitat. More specifically, I aimed to identify: 1) whether the Minnedosa Mallard population was stable; 2) whether growth rates of subpopulations of females using nest tunnel or non tunnel nest locations were increasing, decreasing, or stable; 3) natal sources of yearling female recruits; and, 4) how demographic patterns in adult female survival and yearling recruitment were related to annual population growth rates. To my knowledge, this is the first study to measure simultaneously the relative influence of internal and external sources of productivity on local population growth rates by combining information about origins of yearling female recruits using stable isotope techniques with modern capture-recapture models (Pradel 1996).

3.3 METHODS

3.3.1 *Study area*

Work was conducted in the aspen parkland ecoregion (PARKLAND) of the Prairie Ecozone of Canada (Ecological Stratification Working Group 1995), on 1,036 ha of farmland located in the Rural Municipality of Odanah near Minnedosa, Manitoba, Canada (50°10'N, 99°47'W). Topography ranges from gently rolling hills to relatively flat terrain in a landscape dominated by cereal grain and oil-seed agriculture and containing numerous seasonal, semi-permanent and permanent wetlands. Habitats used by nesting ducks included uplands, hay-land, wetland emergent vegetation, and woodland. Other available nest habitat included 75 man-made nest tunnels suspended over water from metal posts placed on permanent wetlands; most wetlands contained one nest tunnel but some larger wetlands contained up to three. The proportion of tunnels containing nests varied annually within a range of 67-88%.

3.3.2 *Data collection*

During April-August, 2002 - 2005, female Mallards were captured on wetlands using decoy traps (Sharp and Lokemoen 1987) and at nests with drop-door (Weller 1957) or tunnel (Yerkes 1997) traps. Females were then marked with standard leg bands and unique nasal disk color and shape combinations (Lokemoen and Sharp 1985). The

second GSC was sampled from captured individuals to determine age as adult or yearling based on physical characteristics (Krapu et al. 1979). Yearling GSCs were then analyzed for stable hydrogen (δD), nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope composition following the same protocols described in Hebert and Wassenaar (2005a) and normalized relative to keratin and international standards (Wassenaar and Hobson 2003). I could not determine the previous breeding location from feathers of adult females because breeding and molting locations may differ (Hohman et al. 1992). Nests were systematically located in wetlands and uplands from May to July each year using standard searching techniques (Klett et al. 1986). Marked females were resighted using a variable power 80 mm spotting scope (Nikon Corporation, Tokyo, Japan) or recaptured on wetlands or at nests using decoy or nest traps, respectively. Routine resight searches were conducted for marked females on wetlands in the surrounding 1.6 km² area just outside the study area perimeter. Capture at nests occurred during late incubation to minimize its potential influence on nest and female fate. All young were marked with plasticine leg bands at hatch (Blums et al. 1999). Permits were authorized by Canadian Council on Animal Care, Province of Manitoba (2002-04) and University of Saskatchewan (20040021), Canadian Wildlife Service (M002-03), and Environment Canada, Bird Banding Laboratory (sub-permit: 03622QA).

3.3.3 *Yearling natal-origin assignment*

Origin of unmarked yearlings was assigned to boreal (BOREAL), PARKLAND, or United States prairie pothole region (PPR) using a quadratic discriminant function (DF; PROC DISCRIM, SAS Institute Inc., 2008) derived from 130 known-source feather values of pre-fledged Mallard young sampled within these regions during 1999-2001 and 2005 (DWC unpublished data). Predictive performance of the DF was evaluated two ways; 1) using cross-validation and 2) with a test sample of individuals banded as ducklings and recaptured as yearlings at Minnedosa. To simplify modeling, individuals estimated to originate from BOREAL and PPR were pooled as immigrants and then incorporated immigrant and PARKLAND recruitment information into annual population growth rates as described below.

3.3.4 Capture-recapture analysis

Annual encounter histories for marked individuals were constructed based on detection on the study area from 1 April to 31 July each year. Marked individuals were considered detected when seen by at least two different observers in the same year, reducing the chance of misidentification. Individuals were assigned to tunnel and non-tunnel nest location groups based on their first known nest location. Non-tunnel females included those identified attending nests in upland, wetland margin and emergent vegetation, and woodland habitats. Females whose nest location was unknown were pooled with non-tunnel females because this group is likely comprised mostly of failed non-tunnel and a few failed tunnel-nesting females which could not be identified while attending nests. Individuals known to have lost nasal marks were censored from the analysis.

A temporal symmetry extension of a Cormack-Jolly-Seber (CJS) model was used to generate estimates of population growth rates, and apparent annual survival and detection probabilities in Program MARK (Pradel 1996, White and Burnham 1999, Nichols et al. 2000). In temporal symmetry capture-recapture analysis, encounter histories are read forward and backward through time to estimate apparent survival, seniority, and capture probabilities (Pradel 1996, Nichols et al. 2000). Apparent survival (ϕ_i) is the probability that an individual encountered alive during time (i) is alive and present in time ($i+1$). Seniority (γ_i) is the probability that an individual present in time (i) had not entered the population between time (i) and ($i-1$) and capture (p_i) is the likelihood that an individual is captured at time (i) given it is alive and present at time (i) for forward or at time ($i-1$) for reverse analyses, respectively (Pradel 1996). Population growth rate (λ_i) is then estimated as, $\lambda_i = \phi_i / \gamma_{i+1}$ (White and Burnham 1999).

The logit-link function was used for apparent survival and capture probabilities and the log-link for population growth parameters. For model selection, an information-theoretic approach was used to evaluate the relative support for candidate models representing hypotheses about patterns of population growth rates and model-averaged among the candidate set to derive parameter estimates (Burnham and Anderson 1998). The sum of normalized Akaike weights (w_i) was interpreted as a measure of covariate importance in the context of the set of candidate models (Burnham and Anderson 1998).

Models in the candidate set were used to: (1) determine whether the local population and its component subpopulations were increasing, decreasing, or stable; and, (2) evaluate the relative contributions of site and regional sources of recruits to local and subpopulation growth rates. Estimates of λ_i were interpreted as an increasing population when > 1.0 , stable when $= 1.0$, and declining when < 1.0 , given 95% confidence intervals.

I used prior information about female mallard reproductive ecology to implement constraints on model parameters. These constraints included positive correlations between: (1) annual wetland conditions and capture probability (Arnold and Clark 1996, Dufour and Clark 2002); 2) annual increases in wetland abundance and population growth rate (Wilkens et al. 2006); and (3) female and nest mortality rates (Cowardin et al. 1985). Annual counts of study area wetlands during early May, May wetland abundance relative to the previous year (x_{i+1} / x_i), and group-specific nest success estimates were used as indices of local wetland conditions, among-year wetland trends and reproductive performance, respectively (Table 3.2). The inclusion of all three covariates represented a biological null model, and 15 models were evaluated describing population dynamics.

Table 3.2. Covariate description and values used to model annual variation in population growth (λ), apparent survival (ϕ), and capture (p) rates for marked mallards at Minnedosa, Manitoba, 2002-2005. Missing values (-) indicate no year-specific model parameter to constrain.

Parameter	Covariate	Year ¹			
		2002	2003	2004	2005
λ	Relative May wetland abundance ²	-	0.97	1.05	1.15
			20	43	23
	Tunnel-hatched yearlings ³	-	(11)	(24)	(5)
			51	56	27
	PARK-source yearlings ³	-	(28)	(31)	(6)
ϕ			2	5	9
	Immigrant yearlings ³	-	(1)	(3)	(2)
	Tunnel nest success (Mayfield)	0.51	0.44	0.66	-
	Non-tunnel nest success (Mayfield)	0.06	0.03	0.01	-
p	May wetland counts	322	313	328	378

¹ Covariate value in year (*i*) is applied to parameter estimate for year (*i*) .

² Covariate values represent relative estimates of annual May wetland counts (x_{i+1} / x_i).

³ Raw counts of yearling captures (shown in parentheses) were adjusted by annual yearling recapture rates of 0.55, 0.55, and 0.22 for 2003, 2004, and 2005, respectively.

To test the subpopulation hypothesis models were constructed which allowed survival, capture, and population growth rates to vary by tunnel and non-tunnel nest locations, and evaluated support for group differences relative to the biological null. Model variants which allowed annual group-specific growth rates to vary by wetland counts in year ($i+1$) relative to those in year (i) and group-specific capture rates to vary by wetland counts in year (i) were also included (Table 3.2). Other population growth covariates included the number of yearlings known (from band recaptures) to have hatched in tunnels the previous year or the number of immigrant yearlings estimated from isotopic information. Regional sources of yearling female recruits were described as either having natal-origin from within or outside PARKLAND using predictions from feather stable isotope values. Numbers of captured yearling recruits were adjusted by annual recapture rates derived from a separate age-specific CJS analysis of banded ducklings (DWC, unpublished data; Table 3.2). Other models included variants of group-specific population growth rates, constrained by habitat or recruitment covariates, and where each nest location group was allowed to vary independently of the other by different habitat or recruitment covariates. Finally, a global model incorporating effects of group-specific nest success, annual wetland counts, and nest location plus time effects, and a statistical null model with constant survival, capture and population growth rates completed the candidate set.

Apparent survival, capture, or population growth rates did not vary among methods of initial capture (i.e., decoy vs. nest trap) or annual movement from first known nest location group (i.e., stayed vs. moved) in separate analyses, so data were pooled for the analyses described above (DWC, unpublished data). The time between first capture in year (i) and first resight in year ($i+1$) was 30 to 40 days longer for females first marked at decoy traps than at nests. Median, minimum, and maximum days from first capture to first recapture were 360, 286, and 370 for decoy-trapped ($n = 37$) and 325, 272, and 367 for nest-trapped ($n = 48$) females, respectively. However, apparent survival and capture probabilities for females in these groups were similar in a separate time to resight since marking analysis, indicating that the combination of decoy and nest-trap data in nest location groups did not violate homogeneity assumptions (DWC, unpublished data).

3.4 RESULTS

3.4.1 *Recaptures of marked females*

I captured and individually marked 265 adult female Mallards and re-encountered marked individuals on 187 occasions between April 2002 and July 2005. Censoring removed 10 and 9 individuals due to nasal marker loss and those not encountered again within 5 days after first capture (probably transient individuals), respectively, leaving 246 individuals for analysis; 97 were first observed using nest tunnels and 149 were associated with non-tunnel nests. Totals of 244, 350, and 227 ducklings were given plasticine bands at hatch during 2002, 2003, and 2004, respectively. Tunnel and non-tunnel nests produced 204 and 42, 295 and 55, and 220 and 7 ducklings during 2002, 2003, and 2004, respectively. From the marked duckling sample, 12, 27, and 5 were recaptured as yearling females during the 2003, 2004, and 2005 breeding seasons, respectively. Of these, 40 and 4 were hatched from nests in tunnels and non-tunnels, respectively, and 89.0% (44 of 49) were encountered as yearlings during this study. Five females recaptured at ages beyond yearling were not included in yearling recruitment covariate estimates (Table 3.2).

3.4.2 *Yearling natal-origin assignments*

DF cross-validation of feather δD , $\delta^{15}N$, and $\delta^{13}C$ values from pre-fledged ducklings resulted in 78.5% (102 of 130) successful classification of known-source individuals. Region-specific success was 87.3%, 77.1%, and 63.0% of individuals known to have grown feathers in BOREAL, PARKLAND, and PPR, respectively. Of individuals marked as ducklings and recaptured as yearlings at Minnedosa, 93.2% (41 of 44) were successfully predicted to have originated in PARKLAND. Predicted origins of unmarked yearlings indicated that geographic sources varied annually but were primarily of PARKLAND origin (Table 3.3).

Table 3.3. Annual captures of boreal forest (BOREAL), aspen parkland (PARKLAND), and U.S. Prairie Pothole Region (PPR) yearling female recruits estimated from feather δD , $\delta^{15}N$, and $\delta^{13}C$ values during 2002-2005 near Minnedosa, Manitoba, Canada.

Source	Year			
	2002	2003	2004	2005
BOR	10	0	3	2
PARK	35	28	31	6
PPR	2	1	0	0

3.4.3 Model assumptions

There is no direct goodness-of-fit test available for temporal symmetry models and application of forward-time testing may be inappropriate to evaluate of how well data meet assumptions of CJS models (Cooch and White 2007). Violation of the capture-recapture homogeneity assumption can bias initial estimates of population growth rate which then decrease over time as more individuals become marked (Hines and Nichols 2002); however, differences in annual patterns of population growth rates among nest location groups indicated that strong systematic bias is unlikely (Fig. 3.1). Movement of females among nest location groups could confound parameter estimates and my ability to evaluate hypotheses. Nineteen (31%) of 62 marked females detected at nests in multiple years were known to switch locations, with most (89%) movements being from non-tunnel to tunnel nests. If switching was more common than detected, lower support for nest location effects among candidate models would be expected.

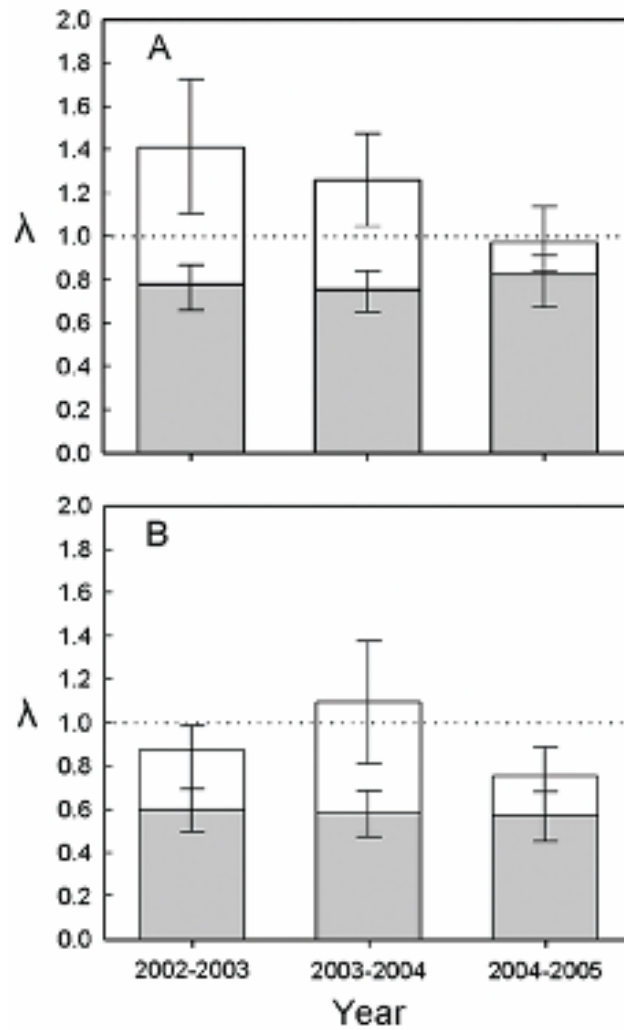


Figure 3.1. Model-averaged estimates ($\pm 95\%$ CI) of annual population growth rate (λ_i) for tunnel (A) and non-tunnel nesting (B) female mallards at Minnedosa, Manitoba, Canada, for 2002-2003, 2003-2004 and 2004-2005. Also shown are apparent survival (ϕ_i , grey fill, $\pm 95\%$ CI) and derived recruitment ($\lambda_i - \phi_i$, white fill) rates. The dashed line represents a stable population growth rate ($\lambda = 1.0$).

Nasal disks do not directly affect survival (Howerter et al. 1997) and permit recapture without physical handling, so marked individuals and measure population parameters were monitored with minimal investigator disturbance. A principal assumption of mark-recapture analysis is that marks are not misidentified or lost. It is likely some marker loss went undetected because the ability to detect marker loss depended upon physical capture of previously-marked individuals, whereas identification of marker retention only required resightings. Marker loss was estimated as 5.3% (10 of 187 recaptures), slightly higher than 3.3% and 2.5% loss rates reported by Lokemoen and Sharpe (1985) and Dufour and Clark (2002), respectively.

3.4.4 *Model selection*

The best-approximating model indicated that population growth rates for tunnel and non-tunnel groups differed, respectively, in relation to annual wetland trends and recruitment of yearling females produced from tunnels (Table 3.4). Based on relative model weights (w_i), this model was more than twice as well supported as the next best model which differed only by inclusion of yearling recruitment from PARKLAND sources for the non-tunnel group. Nest location effects appeared in the top nine models, PARKLAND source recruitment rates appeared twice in the top three, and immigrant source recruits appeared once in the top five. In terms of support for hypotheses, local subpopulation productivity models (T and Park covariates) received 86.8% and models with immigration covariates received 9.1% of support based on cumulative w_i . Models lacking nest location effects were not well supported by data (ΔAIC_c score of < 7.0 , Burnham and Anderson 1998). In the absence of nest location effects, regional recruitment ranked higher than biological null and immigration models (Table 3.4). There was selection uncertainty among candidate models based on ΔAIC_c values so model averaging was used to derive parameter estimates (Burnham and Anderson 1998).

Table 3.4. Model selection results for evaluating sources of demographic rescue of female mallards captured at Minnedosa, Manitoba, Canada, 2002-2005. Population growth (λ) rates were allowed to differ between tunnel (TNL) and non-tunnel (NON) subpopulations, over time (TIME), or as time constant (\bullet). Other covariates included annual wetland counts relative to the prior year (Δ WET), estimates of yearling female recruits produced from within (PARK), or outside (IMM) the aspen parklands, or produced in tunnels (T), both with and without nest location differences among candidate models. Shown for each model are Akaike Information Criterion scores adjusted for small sample size (AICc), relative AICc difference (Δ AICc), relative model weight (w_i), model likelihood (L_i), and number of model parameters (K).

Model ¹	AIC _c	Δ AIC _c	w_i	L_i	K
$\lambda_{\text{TNL}+\Delta\text{WET}, \text{NON}+\text{T}}$	1090.47	0.00	0.45	1.00	9
$\lambda_{\text{TNL}+\Delta\text{WET}, \text{NON}+\text{PARK}}$	1091.89	1.42	0.22	0.49	9
$\lambda_{\text{TNL}+\text{PARK}, \text{NON}+\text{PARK}}$	1092.25	1.78	0.19	0.41	8
$\lambda_{\text{TNL}+\text{TIME}, \text{NON}+\text{TIME}}$ <i>GLOBAL</i>	1094.32	3.85	0.07	0.15	9
$\lambda_{\text{TNL}+\text{IMM}, \text{NON}+\text{IMM}}$	1096.06	5.59	0.03	0.06	8
$\lambda_{\text{TNL}+\Delta\text{WET}, \text{NON}+\Delta\text{WET}}$	1096.25	5.78	0.03	0.06	8
$\lambda_{\text{TNL}+\Delta\text{WET}, \text{NON}+\text{IMM}}$	1097.43	6.96	0.01	0.03	9
$\lambda_{\text{TNL}+\text{T}, \text{NON}+\text{T}}$	1100.96	10.49	0.00	0.01	8
$\lambda_{\text{TNL}, \text{NON}}$	1102.01	11.54	0.00	0.00	7
λ_{PARK}	1110.02	19.55	0.00	0.00	6
λ_{IMM}	1112.85	22.38	0.00	0.00	6
$\lambda_{\Delta\text{WET}}$ <i>BIOLOGICAL NULL</i>	1112.99	22.51	0.00	0.00	6
λ_{T}	1116.01	25.54	0.00	0.00	6
$\lambda_{(\bullet)}$	1116.54	26.07	0.00	0.00	5
$\lambda_{(\bullet)}$ <i>STATISTICAL NULL</i>	1134.55	44.08	0.00	0.00	3

¹ The statistical null was parameterized as time-constant for apparent survival, capture, and population growth rates. All other candidate models included capture rate parameterized as a function of nest location differences plus annual wetland conditions and apparent survival by group-specific nest success rates.

3.4.5 Population growth, apparent survival, and capture

Parameter estimates from the biological null model representing the Minnedosa population were 1.19 (SE: 0.08), 1.06 (SE: 0.05), and 0.91 (SE: 0.07) for population growth rates, and 0.76 (SE: 0.05), 0.74 (SE: 0.05), and 0.80 (SE: 0.05) for apparent survival rates for 2002-2003, 2003-2004, and 2004-2005, respectively. Annual capture probabilities were 0.87 (SE: 0.04), 0.89 (SE: 0.04), 0.86 (SE: 0.04), and 0.70 (SE: 0.09) during 2002-2005, respectively.

Model-averaged estimates of annual population growth rates for the nest tunnel group generally exceeded those of the non-tunnel nesting group except for 2003-2004 (Fig. 3.1); likewise, model-averaged apparent annual survival rate estimates were consistently higher for tunnel-nesting females. Model-averaged estimates for annual capture probabilities were 0.93 (SE: 0.04), 0.93 (SE: 0.04), 0.94 (SE: 0.03), and 0.84 (SE: 0.09) for tunnel and 0.76 (SE: 0.07), 0.79 (SE: 0.07), 0.74 (SE: 0.07), and 0.54 (SE: 0.10) for non-tunnel females during 2002-2005, respectively.

3.5 DISCUSSION

3.5.1 Sources of population rescue

Trends in local population growth rates were consistent with mallard pair counts (Table 3.1) and most closely resembled demographic processes specific to nest tunnels (Fig. 3.1); tunnel-nesting females had consistently higher apparent annual survival rates and produced more yearling female recruits. There was little support for the hypothesis that the mallard population was rescued demographically by yearling immigrants from areas outside the Canadian aspen parklands. Models incorporating aspen parkland source yearling recruits (i.e., covariates T and PARK) were better supported than models involving yearling immigration from distant sources such as the U.S. prairies or Canadian boreal forest (Table 3.4). Yearling origin predictions using feather δD , $\delta^{15}N$, and $\delta^{13}C$ values indicated that most yearling recruits originated from within the aspen parklands (Table 3.3). In general, the spatial distribution of recruit origins among years is consistent with dispersal patterns described for American Crows (*Corvus brachyrhynchos*; Withey and Marzluff 2005) and Tree Swallows (*Tachycineta bicolor*; Winkler et al. 2005).

Population growth rate can be estimated as the sum of survival and recruitment rates so an increase in either of these rates will reduce the contribution needed from the other rate to maintain stability (Pradel 1996). Based on estimates of population growth rates (Fig. 3.1), nest tunnel females increased in 2003 and 2004 and were likely stable in 2005. By contrast, the subpopulation of non-tunnel females declined in 2003 and possibly 2005, and likely increased in 2004. Population growth rates for tunnel-nesting Mallards were driven primarily by high apparent annual survival. Non-tunnel nest locations needed nearly equal contributions from survival and recruitment annually to achieve stability, a pattern consistent with mallard populations elsewhere based on reported apparent survival rates (Arnold and Clark 1996, Dufour and Clark 2002). As a result of a higher apparent survival rate, about half of the recruitment rate was needed to surpass stability in the tunnel population than what might normally be expected. Sources of tunnel-nesting recruits included some tunnel-produced yearlings, but unmarked recruits to the tunnel subpopulation could be renesting or late-arriving females. Most tunnel nests hatched by early June each year, so tunnels became available to other breeding females and second use of nest tunnels by different females has been documented (Chouinard et al. 2005). In contrast, population growth rate for the non-tunnel group was more sensitive to recruitment rates than were tunnel nests because apparent survival rate in this group was consistently lower than that of tunnel-nesting females (Fig. 3.1). Population growth rate for non-tunnel locations was variable because of an apparent reliance on local or regional nest productivity and the return of locally-produced yearling recruits, rates that fluctuated annually during the study (Table 3.2). In addition to nest tunnels, over-water vegetation and idle aspen parkland are other nesting habitats that could potentially produce yearling recruits to occupy “sink” aspen parkland habitats (Arnold et al. 1993, IWWR 1999). However, nests monitored from these habitats had low success and produced no yearling recaptures during this study.

The apparent survival rate estimates for non-tunnel females are similar to rates for female Mallards breeding elsewhere but rates for females using nest tunnels are much higher (Arnold and Clark 1996). Females first detected using nest tunnels averaged 20.3% (SD: 4.3, $n = 3$ years) higher apparent annual survival than females nesting elsewhere, presumably because of lower predation on nesting females. Differences in

apparent survival rates among groups could also reflect higher dispersal of non-tunnel females because permanent emigration cannot be distinguished from death (White and Burnham 1999). Breeding female Mallards are more inclined to disperse following nest failure and so annual differences among nest location groups may reflect the proclivity of females to disperse from low-success habitats (Majewski and Beszterda 1990).

Studies of nest baskets, bales, and tunnels have largely focused on occupancy (Bishop and Barratt 1970, Chouinard et al. 2005) and nest success rates (Doty 1979, Haworth and Higgins 1993, Artmann et al. 2001) with little attention to comparative demography of females using structures versus those nesting elsewhere. Females nesting in tunnels had higher survival rates than females nesting in other locations, and to my knowledge, this is the first demonstration of this difference. In addition to higher hatch rates, tunnel nests typically hatched earlier in the breeding season (median day of year: 164, 10-90 percentile: 146-193, $n = 126$) than non-tunnels (median: 175, 10-90 percentile: 163-196, $n = 19$), perhaps contributing to higher juvenile recruitment rates (Dzus and Clark 1998). However, whether or not females nesting in tunnels could sustain sink populations through higher recruitment or adult survival depends in large part on the proportion of breeding females using tunnels and tunnel success rates, and this problem warrants further investigation.

This study supports the suggestion that tunnels and neighbouring aspen parkland habitats produce most yearling female recruits. The spatial resolution of stable isotope predictions is limited so it cannot be discerned whether predicted aspen parkland recruits originated from undetected nests on or near the study area or further away in the region. However, there was no evidence that demographic rescue by yearlings from boreal forest and U.S. prairie pothole region was a strong determinant of population growth rate in this mallard population. Thus, the source-sink dynamics in this marked mallard population involved fine-scale exchange of yearling female offspring produced by a sub-population on the study site or from nearby areas. I recognize that immigration from more distant sources such as boreal forest might occur in some years. For instance, the highest level of yearling immigration occurred in 2002 (26%, Table 3.3), but I was unable to evaluate its influence because population growth rate could not be estimated for this year.

3.5.2 *Integrating mark-recapture and isotopic information*

Capture-mark-recapture modeling permitted me to evaluate the relative contribution of sub-populations in terms of their respective survival and population growth rates to annual trends in the Minnedosa population. By integrating origin assignment results from feather δD , $\delta^{15}N$, and $\delta^{13}C$ values into capture-mark-recapture models, I was able to constrain population models with an additional recruitment parameter and assess directly the relative support among competing models representing different sources of yearling recruitment with those of local productivity (Table 3.4). The integration of isotopic origin assignments of yearling recruits into capture-mark-recapture models avoided the use of more parameterized multi-state models which necessitates recapturing yearling individuals marked elsewhere. During this study, an adult or yearling female which was marked outside the Minnedosa area was never captured and, given the geographic expanse and size of the mid-continent mallard population in North America, recapturing individuals marked in the Canadian boreal forest or U.S. prairies at a single aspen parkland site seems highly improbable. Even when grouping banding information into large areas, recaptures of mallards and other birds from adjacent areas can be rare (Doherty et al. 2002, Webster et al. 2002).

I was able to integrate comparative demography with ecologically relevant constraints via capture-mark-recapture and tissue stable isotope analyses to test hypotheses about local population dynamics in a migratory bird species. This approach could be applied to other systems where individuals can be marked and tissues sampled non-invasively and may be especially useful, as in this study, where investigators sample highly mobile species at one or multiple sites where the chance of transient recapture is low. While the use of nest tunnels as a subpopulation has obvious management implications, I believe this general approach could be applied to questions about comparative demography in other taxa such as cavity nesting species or has value in assessing the effectiveness of alternative management and conservation interventions.

CHAPTER 4. SOCIAL AND HABITAT CORRELATES OF YEARLING MALLARD IMMIGRATION IN THE CANADIAN PARKLANDS

4.1 ABSTRACT

Conspecific avoidance and attraction are two competing hypotheses about spacing behaviour of individuals and in the last two decades have been used to explain habitat selection by dispersers at fine scales. Advances in stable isotope techniques now allow the movement of individuals to be retraced across broad spatial scales and provide an opportunity to test these hypotheses at broader scales. I used a feather stable isotope approach to evaluate settling patterns of immigrant yearling female mallards at breeding locations across the Canadian aspen parklands during 1993-2000. Settling patterns by immigrants were consistent with predictions of conspecific attraction or avoidance hypotheses, relative to varying habitat conditions. Immigration rates were positively correlated with conspecific breeding pair density and percent perennial nest cover but negatively correlated with percent wetland habitat. Patterns were most consistent with social attraction, but effects were weak. The proportion of female recruits estimated to be long-distant immigrants in 22 aspen parkland breeding populations averaged 9% (range: 0 – 39%). Regional source estimates indicated that 25% and 75% of yearling immigrants originated from the Canadian Boreal Forest and U.S. Prairie Pothole Region, respectively and suggest a high degree of connectedness among breeding regions as a result of long-distance natal dispersal. I suspect that this connectedness may serve to avoid extinction risks when regional habitat suitability is unstable.

4.2 INTRODUCTION

Resource quality and social interactions are two primary factors affecting the distribution of individuals across habitats (Fretwell and Lucas 1970, Stamps 2001, Fletcher 2007). Two social conditions which could influence the spatial distribution of settling individuals include conspecific attraction or avoidance (Stamps 2001). Under the social attraction hypothesis, dispersing individuals may interpret conspecific abundance as a positive cue of habitat quality (Fletcher 2007), predator avoidance, or

mate access (Wagner 1997), or alternatively, as a negative cue of higher fitness costs from increased resource competition. In the absence of social influences, the distribution of individuals would be expected to resemble gradients in resource quality because individuals should settle in habitats that maximize fitness. However, individuals settling in unfamiliar areas must choose habitats using environmental cues which may or may not be linked with a successful outcome (Schlaepfer et al. 2002, Kristan 2003).

Dispersal by individuals has been linked to environmental instability (Imms and Hjermmann 2001, Studds et al. 2008) such that emigration rates increase as local resource abundance or quality declines. If the status of resources is the mechanism driving dispersal rates then settlement rates of dispersers at destinations (i.e., immigration rates) should be positively correlated with local habitat conditions. However, the relationships between habitat quality, social factors and where immigrants choose to reside across broad scales (i.e., > 500km) are unknown, primarily due to constraints in determining the residency status of unmarked individuals. The origin of unmarked individuals can be reliably traced across broad spatial scales using intrinsic biological markers such as tissue stable isotope values (Hebert and Wassenaar 2005a). This is possible because consumers incorporate stable isotopes from local food webs into growing tissues and tissue values can then be compared with geographic patterns (review by Rubenstein and Hobson 2004). For example, molt chronology and sequence have been described for many bird species allowing for the sampling of specific feather tracts to link individual breeding performance to winter habitat use (Marra et al. 1998). The isotopic approach may be especially useful to delineate geographic sources of unmarked juvenile recruits because metabolically inert tissues such as claws and feathers are often suitable for sampling several months after young leave natal areas. Thus, the isotopic approach can quantify dispersal and has potential for addressing unresolved questions about factors affecting distributions of breeding birds.

In duck species, female dispersal and fidelity (the complement to dispersal) rates are generally related to age and habitat quality (Arnold and Clark 1996, Arnold et al. 2002, Blums et al. 2003). Adult female ducks typically are breeding-site faithful and yearlings (one-year old individuals) typically have lower rates of fidelity to natal areas

(Dufour and Clark 2002, Doherty et al. 2002). In addition to detection problems, lower recapture rates of yearlings on natal sites may be the result of greater dispersal proclivity (Anderson et al. 1992). Thus, most female immigrants in breeding populations are likely yearlings.

The distribution of breeding North American mallards (*Anas platyrhynchos*) is positively correlated with wetland conditions (Krapu et al. 1983, Johnson and Grier 1988), a resource which can be highly dynamic at local and regional scales (Wilkens et al. 2006) due to inter-seasonal fluctuations in snowmelt runoff, summer precipitation, and evapotranspiration rates (Murkin et al. 2000). Periods of severe drought in the US prairies results in “over-flights” by breeding-pairs into more northern breeding regions causing local populations to increase (Johnson and Grier 1988). Presumably, large increases in breeding-pair densities in the Canadian prairies are at least partly due to immigration because many local populations lack sufficient reproductive success for stability or growth (Greenwood et al. 1995). The extent to which local mallard populations might be maintained by immigration is unknown and if this process involves bird movements over large areas, this would suggest greater connectedness amongst regions of North America than is currently recognized. Large-scale mark-recapture studies conducted across species’ distributions are logistically difficult and expensive (Clark et al. 2004). Despite exceptional numbers of banded mallards, most are >1 year old, male, and banded at accessible sites in late summer. By contrast, isotope signatures of yearling females provide a measure of natal origin for *all* females captured at breeding sites.

Mallard breeding-pairs exhibit resource defence behaviour and success in contests generally favours pairs composed of older birds (Dzubin 1957). In lieu of adults, breeding yearlings with local familiarity might be expected to have an advantage over yearling competitors with no prior experience in the area. Thus, if immigrants are pre-empted from settling, the social avoidance hypothesis predicts that the composition of immigrant yearlings will be inversely related to the size of the breeding population. Alternatively, the social attraction hypothesis allows territorial behaviour to represent a positive cue of habitat quality for individuals not familiar with local resources and so predicts that immigrants will be more abundant in high-density populations until

populations become saturated (Allee 1951, Stamps 2001). There is some evidence of social attraction in mallards occurring at the wetland scale (Pöysä et al. 1998) but whether settlers had prior knowledge of local habitat quality was not evaluated.

Little is known about how habitat or social cues are related to the distribution of yearling mallards among breeding areas, or exchange of individuals among major biomes. Therefore, my first objective was to delineate the natal origin of yearling female mallards at multiple breeding sites across the Canadian prairies. My second objective was to evaluate how immigration rates were related to varying social and habitat conditions at breeding locations. This is the first study to quantify immigration rates of yearling females in breeding populations across broad spatiotemporal scales and to evaluate the influence of social and habitat cues on immigration patterns at coarse spatial scales. Identifying spatial determinates of immigrant distributions has implications for population ecology and conservation and represents the precursor to understanding the adaptive process of habitat selection (Clark and Shutler 1999) as it relates to site familiarity.

4.3 METHODS

During April to early May, 1993-2000, 721 yearling female mallards were captured in decoy traps and radio marked at 22 breeding locations across the Canadian prairies (Emery et al. 2005; see Table 4.1). These females represent a sub-sample of >1,200 yearlings from 27 sites with $\geq 90\%$ probability of belonging to this age class based physical characteristics of greater-secondary covert feathers (GSC; Krapu et al. 1979).

Table 4.1. Descriptive attributes of sampling locations including year, degree latitude (LAT, ° N) and longitude (LONG, ° W), size (km²), mallard breeding-pair density (km²) (PAIRS), percent habitat in wetlands (PONDS) and perennial nesting cover (NCOV), and estimates of yearling recruits from Canadian boreal forest (BOR) and aspen parklands (PARK), and U.S. prairie pothole region (PPR) determined from feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values.

Location	Year	LAT	LONG	SIZE	PAIRS	PONDS	NCOV	BOR	PARK	PPR
Punnichy, SK	1993	51.3	-104.3	55.4	5.1	5.2	33.0	2	15	0
Belmont, MB	1994	49.4	-99.5	65.1	4.5	11.4	52.2	0	18	3
Davis, SK	1994	53.2	-105.6	67.7	7.6	10.4	48.7	0	23	0
Kutawagon Lake, SK	1995	51.4	-104.2	67.1	3.4	10.3	36.3	0	28	0
Baldur, MB	1996	49.4	-99.3	67.2	7.5	14.1	58.5	0	37	0
Parkside, SK	1996	53.2	-106.6	66.0	4.4	5.8	37.6	0	32	0
Pine Lake, AB	1996	52.2	-113.4	65.6	5.7	8.7	74.1	2	17	0
Allan Hills West, SK	1997	51.7	-106.1	65.5	14.5	9.1	39.7	1	28	2
Elnora, AB	1997	52.0	-113.3	65.9	5.6	7.9	83.5	5	19	2
Mixburn, AB	1997	53.1	-111.4	65.7	4.9	10.7	50.5	0	31	2
Willowbrook, SK	1997	51.2	-102.9	66.8	6.5	7.7	41.1	1	30	0
Donalda, AB	1998	52.6	-112.6	65.8	14.3	11.8	38.9	2	32	3
Farrerdale, SK	1998	51.5	-105.9	65.7	6.2	5.8	34.3	3	21	1
Jumping Deer Creek, SK	1998	51.2	-104.1	65.6	10.2	11.6	69.1	0	30	0
Minnedosa, MB	1998	50.2	-99.9	67.0	10.4	14.4	40.8	0	56	2
Allan Hills East, SK	1999	51.6	-105.9	65.7	16.2	9.6	56.4	0	14	9
Kinsella, AB	1999	52.9	-111.7	65.7	8.5	6.9	62.3	0	21	0
Red Deer, AB	1999	52.4	-112.4	65.7	10.3	10.7	69.3	0	16	2
Allan Hills North, SK	2000	51.7	-106.2	66.3	12.2	8.8	36.3	0	16	2
Holmfield, MB	2000	49.2	-99.5	68.0	10.2	23.4	67.5	0	25	1
Leask, SK	2000	53.1	-106.9	65.2	3.4	11.0	36.0	0	23	1
Prince Albert, SK	2000	53.1	-105.5	67.0	9.7	14.4	57.1	1	20	1

Yearling GSCs were analyzed for stable sulfur ($\delta^{34}\text{S}$), hydrogen (δD), nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope composition due to their reliability in regional origin assignment (Hebert and Wassenaar 2005a, DWC unpublished data). Feathers were processed to determine isotopic values following protocols described in Hebert and Wassenaar (2005a) and normalized relative to keratin and international standards (Wassenaar and Hobson 2003). Measurement error was $\pm 0.5\text{‰}$, $\pm 2.0\text{‰}$, $\pm 0.2\text{‰}$, and $\pm 0.1\text{‰}$, and for $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$, respectively. Analysis for $\delta^{34}\text{S}$ and δD was conducted at the National Water Research Institute, Saskatoon, Saskatchewan, Canada. Feather $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were analyzed at the Department of Soil Science, University of Saskatchewan, Saskatoon.

Yearling females were assigned to the Canadian boreal forest (BOREAL), Canadian aspen parklands (PARKLAND), or United States Prairie Pothole Region (PPR) (Ecological Stratification Working Group 1995, Ducks Unlimited, Inc., unpublished data) using a quadratic discriminant function (DF; PROC DISCRIM, SAS Institute Inc., 2008) derived from feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values of 138 pre-fledged mallard sampled within these regions during 1999-2001 and 2005 (DWC unpublished data). Feathers from flightless young should reflect local food web isotopic signatures since these feathers could not have been grown elsewhere. Predictive performance of the DF was evaluated using cross-validation where functions were recalculated routinely withholding each individual in the sample and then used to estimate each individual's assignment (PROC DISCRIM, SAS Institute Inc., 2008). Residency status was then estimated as IMM or resident (RES) based on whether individuals were assigned to PARKLAND in the DF. To account for assignment uncertainty, I analyzed individuals with regional membership probability of >0.70 .

PROC GENMOD (SAS Institute, Inc., Cary, NC) was used to evaluate variation in the ratio of IMM:total captured yearling recruits at each study area (SAR) using logistic regression (e.g., Hazler 2004, Arnold et al. 2007). The relative importance of different models describing social and habitat conditions was assessed using Akaike's Information Criterion adjusted for sample size and over-dispersion (QAIC_c; Burnham and Anderson 1998). The sum of normalized Akaike weights (w_i) among candidate

models was interpreted as a measure of covariate importance and model-averaging was used to derive parameter estimates (Burnham and Anderson 1998).

An *a priori* set of candidate models was constructed using information about breeding mallard distributions and reproductive ecology. Covariates believed to be important to the immigrant distribution across PARKLAND study sites included wetland conditions in the PPR (Johnson and Greir 1988) and local breeding-pair density (PAIRS), as well as site-specific wetland abundance and amount of perennial nesting cover (Greenwood et al. 1995, Krapu et al. 1997, Reynolds et al. 2001). Annual PPR wetland conditions during the study were characterized using stratum-specific ($n = 7$ strata) wetland density (wetlands per km^2 ; hereafter, PPR-PONDS) estimates from annual CWS-USFWS waterfowl survey (data source: <http://mbdcapps.fws.gov/mbdc/index.html>). Analysis of variance (ANOVA) was used to evaluate whether annual differences in PPR-PONDS warranted inclusion in candidate models. At each SAR, estimates of PAIRS were determined from multiple surveys conducted in early May (Dzubin 1969) and wetland (PONDS) and perennial nesting cover (NCOV) were estimated as a percentage of SAR using aerial photos described by Devries et al. (2003).

4.4 RESULTS

4.4.1 Yearling regional-origin assignments

DF cross-validation of feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values from pre-fledged ducklings resulted in 81% (112 of 138) successful classification of known-source individuals. Region-specific assignment success was 90%, 82%, and 70% of individuals known to have grown feathers in BOREAL, PARKLAND, and PPR, respectively. Relative to prior distribution of known-source cases, correct classification was 2.5, 2.3, and 2.4 times better than chance for BOREAL, PARKLAND, and PPR regions, respectively. DF estimated 33, 638, and 54 yearling individuals to originate from BOREAL, PARKLAND, and PPR, respectively. Thus, overall 87 and 634 individuals had residency status of immigrant and resident, respectively, or 48 and 552, respectively, when applying a 0.70 threshold for inclusion. Differences in model selection occurred among raw and constrained membership data sets indicating some

influence of assignment uncertainty on results, so I report the most conservative results from the data with >70% assignment certainty.

4.4.2 Model selection

Annual values of PPR-PONDS did not vary during the study (ANOVA, $F_{7,69} = 0.96$, $P = 0.47$) and were not considered further. The global model included SAR PAIRS, PONDS, NCOV, and an interaction between PAIRS and PONDS. This model provided some evidence of lack of fit (deviance/df = 2.4) so evaluation of candidate models was standardized using the square root of this value (Littell et al. 2002).

An intercept-only model provided the best fit to the data. Other models with PAIRS, PONDS, and NCOV covariates, singly or in combination, were also plausible based on ΔQAIC_c values of <5.0 (Table 4.2). Cumulative QAIC_c weights among covariates indicated that PAIRS was slightly more important than PONDS and that both were >4 times more important than NCOV (Table 4.2). There was no support for an interaction between PAIRS and PONDS. Model-averaged estimates were imprecise and indicated that PARKLAND immigration rates were correlated negatively with PONDS but were associated positively with PAIRS and NCOV (Table 4.3).

Table 4.2. Model selection results for the association of site-specific ratio of immigrant to resident yearling recruits with local breeding-pair density (PAIRS), percent habitat in wetlands (PONDS) and nest cover (NCOV) and intercept (INTERCEPT) either singly in additive (+) or interaction (*) combinations. Shown also are number of model parameters (K), Akaike's Information Criterion adjusted for over-dispersion and small sample size (QAIC_c), model likelihood (L_i) and relative weight (w_i).

Model	K	QAIC_c	ΔQAIC_c	L_i	w_i
INTERCEPT	2	61.95	0.00	1.00	0.43
PAIRS	3	63.23	1.28	0.53	0.23
PONDS	3	64.05	2.10	0.35	0.15
PAIRS+PONDS	4	64.98	3.03	0.22	0.09
PONDS+NCOV	4	66.30	4.35	0.11	0.05
PAIRS+PONDS+NCOV	5	67.31	5.36	0.07	0.03
PAIRS+PONDS+PAIRS*PONDS	5	68.38	6.43	0.04	0.02
PAIRS+PONDS+PAIRS*PONDS+NCOV	6	71.08	9.13	0.01	0.00

Table 4.3. Model-averaged regression coefficients (β), standard errors (SE), and cumulative normalized weights (Σw) for social and habitat covariates of the ratio of immigrant to resident recruit at 22 breeding locations in the Canadian aspen parklands, 1993-2000.

Covariate	β	SE	Σw
Intercept	-2.59	0.60	1.00
PAIRS	0.12	0.08	0.37
PONDS	-0.12	0.09	0.33
PAIRS*PONDS	0.01	0.04	0.02
NCOV	0.02	0.02	0.08

4.5 DISCUSSION

4.5.1 *Correlates of immigration*

Patterns in yearling mallard immigration rates at aspen parkland breeding locations were evaluated whether they were consistent with predictions of social attraction or conspecific avoidance hypotheses, relative to habitat conditions. Effects of breeding-pair and wetland densities, and perennial nest cover were negligible (Table 4.3), providing only weak evidence that probability of a yearling immigrant settling in aspen parkland breeding populations increases on sites with higher breeding-pair densities and amount of perennial nesting cover but lower wetland abundance. Collectively, these results are most consistent with social attraction (Stamps 1991, Stamps 2001). That immigrant settling patterns may follow social attraction rules resemble patterns observed in Scandinavian mallards, where settlers were more likely to use wetlands already occupied by conspecifics (Pöysä et al. 1998). Social attraction for breeding habitat selection has also been demonstrated in other vertebrates (Stamps 1991, Etterson 2003, Doligez et al. 2004) and invertebrates (Jeanson and Deneubourg 2007, Lecchini et al. 2007).

Reproductive effort and success in mallards is positively correlated with wetland conditions (Johnson and Grier 1988) so breeding individuals would be expected to settle where conditions are most favourable for nest success. It has been suggested that higher

survival in younger female mallards during dry habitat conditions is related to a reduction in breeding propensity (Dufour and Clark 2002). If immigrant yearlings are less likely to breed due to physiological constraint or individual restraint they might be expected to congregate in areas best suited for survival. Alternatively, there is evidence that social attraction increases fecundity of settlers, especially in fragmented landscapes, by lowering search costs to survival (Fletcher 2006). In either case there is a potential benefit by aggregating with conspecifics. Whether social attraction leads to higher fitness in yearling immigrant mallards warrants further investigation.

That immigration rates were negatively correlated with pond abundance was somewhat surprising, given that I expected these rates would be positively correlated with wetland inundation among study areas due to the positive association of wetland abundance on mallard breeding pair distribution, breeding effort and success (Johnson and Grier 1988, Drever et al. 2004). In a review of animal release studies, Stamps and Swaisgood (2007) found that translocated animals frequently dispersed great distances and settled in habitats or environments similar to which they had been raised or experienced; a behaviour attributed to “habitat imprinting” (Stamps 2001). The U.S. prairie pothole region has consistently lower wetland density than the Canadian prairies and aspen parklands (see Wilkens et al. 2006, DWC unpublished data) and nesting habitat is considered less fragmented at the landscape scale in U.S. prairie pothole region; a pattern attributed to differences in Canadian and U.S. agricultural policies (Reynolds et al. 2006). Thus, immigrants searching for suitable habitats may find aspen parkland areas with more perennial cover but fewer wetlands to resemble more closely their natal region and thus perceive them as adequate in lieu of wetter locations. An alternative is that immigrants are forced to settle in areas with fewer wetlands by territorial behaviour. The evidence of a weak positive association with breeding pairs is more consistent with habitat imprinting than competitive exclusion.

Earlier work on waterfowl distributions indicate that when the U.S. prairie pothole region experiences drought that mallards and other waterfowl continue migrating to northern areas where wetland conditions are better (Johnson and Grier 1988). I was unable to incorporate whether variation in immigration rates at aspen parkland sites was related to wetland conditions in southern U.S. prairies because

wetland conditions in the U.S. prairie pothole region were above the long-term average and were relatively stable during this study (see Wilkens et al. 2006). However, drought in the U.S. prairie pothole region must be an important mechanism driving immigrants north to aspen parkland areas.

That the marked population is representative of the yearling mallard populations at breeding locations is one of several assumptions underpinning my analyses. There is no prior biological expectation for capture heterogeneity to occur among immigrants and residents, so I believe that results from marked individuals are relevant to patterns in mallard populations in the Canadian aspen parklands. Another assumption pertains to the reliability of residency assignments. Hebert and Wassenaar (2005a) demonstrated that the reliability of feather stable isotope predictions of individual regional origin can be >85% across broad spatial scales and my results approximate this rate but at a finer spatial scale. The isotopic approach assumes that assignments are robust to temporal variation in local food web stable isotope values, an assumption which has not been evaluated and seems unlikely to be valid at least for precipitation driven deuterium values (Appendix A). I attempted to account for sources of assignment bias by restricting the analysis to only include females with a $\geq 70\%$ posterior assignment probability.

The social avoidance hypothesis assumes that individuals are pre-empted from residing in habitats occupied by conspecifics. As Pöysä et al. (1998) pointed out, high nest densities on islands and home range overlap in mallards suggests that territory intruders are not truly excluded from habitats where others are established. These authors also demonstrated that new arrivals were not pre-empted from wetlands occupied by unnaturally high pair densities so it seems unlikely that immigrants would be excluded at the broader scale of this study if they are not excluded at fine spatial scales. The social attraction hypothesis assumes that dispersing individuals cannot accurately assess habitat cues at destinations and therefore rely on the distribution of conspecifics as a cue to habitat quality. Yearling mallards have no prior breeding experience to aid habitat evaluation and it seems unreasonable to expect immigrant yearlings would be adapted to local habitat cues at distant locations. Furthermore, nest success in mallards and other dabbling ducks (*Anas spp.*) is highly variable across

multiple spatial and temporal scales (Klett et al. 1988, Greenwood et al. 1995, McKinnon and Duncan 1999) making it likely difficult for even the experienced breeder to predict (Clark and Shutler 1999). Whether immigrant fitness is positively correlated with habitat or social cues is a topic evaluated elsewhere (Chapter 5).

4.5.2 *Movements among biomes*

Boreal forest has been historically characterized by low breeding-pair densities (Johnson and Grier 1988, Wilkens et al. 2006) with presumed consistent but low levels of breeding success (Calverley and Boag 1977). I estimated that ~25% (12 of 47) of immigrants to aspen parkland sites were produced in boreal forest. This rate is similar to that reported for mallards in other aspen parkland populations (Coulton and Clark 2008) and suggests that western boreal forest may be a more important source of recruits than previously believed. Although breeding pair densities are lower in boreal than U.S. prairie biomes, the long-term average indicates that approximately twice as many ducks occupy the former biome because of its vast area (Wilkens et al. 2006). In contrast, the U.S. prairie pothole region is believed to be highly productive due to favourable wetland and grassland-retention policies (Reynolds et al. 2001, Reynolds et al. 2006), but with more variable wetland abundance. Overall, ~75% of yearling immigrants originated from U.S. prairie pothole region. Thus, these source-specific immigrant rates are consistent with historical perceptions of lower and higher productivity in the Canadian boreal forest and U.S. prairie pothole region, respectively.

Immigration can serve an important role for population persistence in unstable environments (Stacy and Taper 1992). Habitat conditions for prairie nesting ducks are highly variable in space and time due natural and anthropogenic impacts. Furthermore, natural habitat degradation and loss can be caused by local or regional drought (Murkin et al. 2000) or drainage for agricultural production (Lynch et al. 1963). Thus, natal movements among major biomes may be mechanisms which allow mallards and other species to repopulate temporally unsuitable habitats and avoid extinction risks.

The ratio of yearling mallard immigrants to natal-resident recruits in breeding populations in the Canadian aspen parklands was positively correlated with social cues, as predicted by the conspecific attraction hypothesis. However, considering the

importance of wetlands to mallard vital rates, it seems unreasonable to expect that settlement patterns by yearling immigrants are based solely on conspecific density. We suspect that settling patterns by individuals dispersing long distances among biomes involves assessing cues across multiple spatial scales and, in particular, breeding environments encountered in southern portions of breeding ranges during northward migration.

CHAPTER 5. CONSEQUENCES OF NATAL DISPERSAL IN YEARLING FEMALE MALLARDS: A TEST OF THE SITE FAMILIARITY HYPOTHESIS

5.1 ABSTRACT

According to the site familiarity hypothesis, philopatric individuals have higher fitness than do immigrants because site-faithful individuals are more familiar with local cues and resources. Of the few studies that have evaluated this hypothesis, fine scale studies of life-time reproductive success in songbirds indicate that immigrants do as well or worse than natal residents, but patterns at larger scales are unknown. I tested whether locally-produced individuals had higher reproductive success than immigrants using information about natal origins and reproductive fates of 375 radio-marked yearling mallards (*Anas platyrhynchos*) monitored at 15 study sites across the Canadian aspen parklands, during 1993-2000. An origin assignment model based on multiple stable isotopes of feathers correctly assigned 81% (112 of 138) of known-source yearlings to place of natal origin; region-specific rates ranged from 70 - 90%. Using nest fate (hatched versus fail) as a proxy for fitness, logistic models were evaluated on a local (resident versus immigrant) scale. In the absence of residency effects, yearling hatch rates showed a negative relationship with breeding-pair density when local wetland conditions were excellent and a positive relationship when poor. Yearling breeding probability was positively correlated with local wetland conditions. When residency status was considered, the best approximating nest fate model included an interaction between site-specific breeding pair and wetland densities but lacked differences due to residency status. Bootstrap-derived fitness estimates from the top model incorporating residency effects were 0.21 (95% CI: 0.10 - 0.34) and 0.18 (95% CI: 0.13 - 0.22) for immigrants and residents, respectively. In contrast to results for other bird species, there was little evidence that reproductive success differed among philopatric versus immigrant yearlings. However, at low pair densities, immigrants generally had higher nesting success than did residents whereas residents performed better than immigrants at high breeding pair densities during environmental stress. Thus, benefits of dispersal were most pronounced when immigrants encountered good wetland conditions and low pair densities.

5.2 INTRODUCTION

Dispersal behaviour has presumably evolved because dispersing individuals have higher subsequent fitness than do individuals that stay on natal or previous breeding areas (reviewed by Johnson and Gaines 1990). Individuals that move to unfamiliar areas must select habitat using social and environmental cues which may not be reliably linked with higher fitness (Schlaepfer et al. 2002, Kristan 2003). Under the site familiarity hypothesis, philopatric individuals have an advantage of previous experience with the local environment and can potentially avoid pitfalls of misleading cues. This is because residents are more familiar with the location of high quality resources, are better able to evade local predators, reduce intraspecific competition, or benefit from close proximity to kin (Greenwood 1980, Anderson et al. 1992). Thus, the site familiarity hypothesis predicts that fitness will be greater for locally-experienced versus naïve individuals. Individuals with previous experience may also benefit from earlier reproductive effort and/or success due to differential acquisition of preferred space or other resources.

Tests of the site familiarity hypothesis have been limited to fine scale studies of lifetime reproductive success in seven different passerines (see Marr et al. 2002) where the likelihood that an unmarked individual was an immigrant could not be assessed and only recently has dispersal distance been considered (Hansson et al. 2004). In general, these investigations show sex-dependent residency effects and, in the more philopatric gender, that immigrants do worse than or only as well as philopatric individuals (Pärt 1994, Julliard et al. 1996, Verhulst and van Eck 1996, Bensch et al. 1998, Orell et al. 1999, Hansson et al. 2004). The strength of these studies is the ability to track individual fitness through time. However, whether these patterns are broadly applicable requires investigation at broader scales and in other animals which differ in life history traits. How dispersing individuals respond to selective pressures relative to non-immigrants in local environments is key to understanding the role of dispersal in population dynamics and the evolution of dispersal behaviour (Johnson and Gaines 1990).

The origin of unmarked individuals can be reliably traced across broad spatial scales using intrinsic biological markers such as tissue stable isotope values (Hebert and Wassenaar 2005a). This is possible because consumers incorporate stable isotopes from local food webs into growing tissues and tissue values can then be compared with geographic patterns (reviewed by Rubenstein and Hobson 2004). For example, molt chronology and sequence have been described for many bird species allowing for the sampling of specific feather tracts to link individual breeding performance to winter habitat use (Marra et al. 1998). The isotopic approach may be especially useful to delineate the geographic sources of unmarked individuals because metabolically inert tissues such as claws and feathers may remain suitable for sampling for several months after departure from the location where grown. The isotopic approach can be used to determine residency status and, hence, has potential for resolving questions about fitness differences related to site familiarity and how components of fitness may be affected by processes such as density dependence.

The regulation of North American mallards by density dependence has been demonstrated at broad scales (Sheafer 1998, Miller 2000, Viljugrein et al. 2005, Saether et al. 2008) but patterns at more local scales are less clear (Vickery and Nudds 1984). Evaluation of fall harvest age ratios indicates that mallard (*Anas platyrhynchos*) recruitment may be regulated by density dependence (Kaminski and Gluesing 1987); however, which components of the reproductive cycle are affected remain unknown. European studies indicate density dependence influences recruitment via effects on nesting and fledging success (Hill 1984, Elmberg 2003, Elmberg et al. 2005). Evidence of density dependence specific to these rates in North American mallards is lacking but potentially represents a breeding-ground link between density dependence in abundance and fall harvest age ratio measures.

In duck species, dispersal and fidelity (the complement to dispersal) rates are generally related to age and habitat quality (Arnold and Clark 1996, Arnold et al. 2002, Blums et al. 2003). In female ducks, breeding-site fidelity in adults is usually higher than natal fidelity rates of yearlings (one-year old individuals) (Anderson et al. 1992, Arnold and Clark 1996). In addition to detection problems, lower recapture rates of yearlings on natal sites may be the result of greater dispersal proclivity (Anderson et al.

1992). Reasons for dispersal include habitat loss, resource competition, variability in habitat quality and inbreeding avoidance (Anderson et al. 1992, Dieckmann et al. 1999). Yearling females dispersing in search of apparently “good” breeding habitat may be vulnerable to ecological traps, resulting in poor reproductive and survival decisions (Schlaepfer et al. 2002).

Reproductive effort and nest success in North American mallards vary geographically in the same year and between years (Klett et al. 1988, Greenwood et al. 1995, McKinnon and Duncan 1999, Drever et al. 2004). There is also evidence that breeding-season site fidelity and survival in female mallards varies with age (Reynolds et al. 1995, Dufour and Clark 2002, Devries et al. 2003). Variation in reproductive success and age-related survival may reflect differences associated with benefits of residency status and site-familiarity of yearlings. Reproductive fate may represent a relevant way to assess relative fitness differences among resident and non-resident yearlings exposed to the same selective pressures since production of offspring demonstrates gene flow among generations (Johnson and Gaines 1990). Yearling female mallards retain greater-secondary covert feathers (GSC) grown as ducklings until after their first breeding season (Heitmeyer 1989). Thus, natal origins, and hence residency status, of yearling females can be ascertained by measuring stable isotope values in GSC feathers when sampled at breeding areas. The site-familiarity hypothesis predicts that yearling females which show natal fidelity will have higher fitness than immigrant yearlings due to differential experience with the local environment. Additionally, residents might nest and/or hatch broods earlier than immigrants as a benefit of familiarity with local nest habitat quality, resulting in higher recruitment rates (e.g., Dzus and Clark 1998).

Little is known about the exchange of individuals across broad spatial scales (i.e., >500 km) and how dispersal to unfamiliar environments influences subsequent survival or reproductive performance. My first objective was to examine relationships between breeding and hatch rates of yearling female mallards in relation to pair density and habitat quality. My second objective was to determine the residency status of yearling female mallards monitored for reproductive fate at 22 sites across the Canadian aspen parklands during 1993-2000. My third objective was to test whether fitness of

resident yearlings was higher than non-residents, as predicted by the site-familiarity hypothesis. This approach represents a unique attempt to link natal origin using stable isotope methods with components of fitness to evaluate consequences of natal dispersal across broad spatiotemporal scales in mid-continent North America.

5.3 METHODS

During mid to late April, 1993-2000, 724 yearling female mallards were captured in decoy traps and radio marked at 22 breeding locations across the Canadian prairies. These females represent a sub-sample of >1,500 yearlings from 27 sites with an estimated $\geq 90\%$ probability of belonging to this age class based physical characteristics of greater-secondary covert feathers (GSC; Krapu et al. 1979). Marked females were tracked daily to determine survival and reproductive fate using radio-telemetry techniques described by Devries et al. (2003). Only females were considered in this study because few male mallards return to the same breeding areas.

Yearling GSCs were analyzed for stable sulfur ($\delta^{34}\text{S}$), hydrogen (δD), nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope composition because these isotopes can be used reliably to assign birds to a regional origin (Hebert and Wassenaar 2005a). Feathers were processed to determine isotopic values following protocols described in Hebert and Wassenaar (2005a) and normalized relative to keratin and international standards (Wassenaar and Hobson 2003). Measurement error was $\pm 0.5\text{‰}$, $\pm 2.0\text{‰}$, $\pm 0.2\text{‰}$ and $\pm 0.1\text{‰}$ for $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values, respectively. Analysis for $\delta^{34}\text{S}$ and δD was conducted at the National Water Research Institute, Saskatoon, Saskatchewan, Canada. Feather $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were analyzed at the Department of Soil Science, University of Saskatchewan, Saskatoon.

Yearling females were assigned to the Canadian boreal forest (BOREAL), Canadian aspen parklands (PARKLAND), or United States prairie pothole region (PPR) (Ecological Stratification Working Group 1995) using a quadratic discriminant function (DF; PROC DISCRIM, SAS Institute Inc., 2008) derived from $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values in feathers of 138 pre-fledged mallard young sampled within these regions during 1999-2001 and 2005 (DWC, unpublished data). Feathers from flightless young should reflect local food web isotope signatures since these feathers could not have

been grown elsewhere. Predictive performance of the DF was evaluated using cross-validation. Residency status was then assigned as immigrant (IMM) or resident (RES) based on whether individuals were assigned to PARKLAND in the DF. To reduce effects of origin assignment uncertainty, I only analyzed individuals with regional membership probability ≥ 0.70 .

Hatch rate (h_i) was defined as the probability that females survived and hatched at least one egg. Individuals were included if there was certainty that a hatched nest was not missed ($n = 665$). Breeding propensity (b_i), the probability that an individual nested, was estimated from a sample of females with high certainty that all nest attempts were detected ($n = 426$). Logistic regression was first used to estimate h_i and b_i for all yearling females with respect to breeding-pair density, wetland density and their interaction to test for density dependence. The same candidate models were then considered relative to estimated yearling female residency status to examine site familiarity effects (PROC GENMOD; SAS Institute Inc., 2008). An estimate of the variance inflation factor (\hat{c}) from the most parameterized model was used as a measure of goodness-of-fit of the data to the candidate set for each analysis, where $\hat{c} = 1.0$ is ideal fit (Burnham and Anderson 1998). Model selection was completed using an information-theoretic approach to evaluate the relative support for candidate models representing my hypotheses, and model-averaging among the candidate set as used to derive parameter estimates (Burnham and Anderson 1998). The inverse-link and Delta Rule were used to transform logit estimates and standard errors to the probability scale, respectively (Littell et al. 2002).

A bootstrap approach was used to identify h_i and b_i distributions for IMM and RES and to derive group-specific 95% confidence limits from an equal number of simulations (i.e., to reduce effects of highly unbalanced group sample sizes). In the bootstrap routine, individuals from each group were randomly selected with replacement, until equal to the original group sample size. Least-square mean estimates of h_i and b_i were then derived from these data using the most parsimonious model containing residency effects. Random sampling and estimation steps were repeated 1,000 times. Differences between IMM and RES for h_i and b_i distributions were evaluated using a two-sample Kolmogorov-Smirnov test. I conducted an *a posteriori*

evaluation of study area h_i rates to identify sites where either IMM or RES individuals were favoured or similar. Group-specific rates at sites were considered higher if h_i differences exceeded 10%; otherwise they were similar. Sites were then pooled into strata for further analyses according to whether they favoured IMM or RES or were neutral. Sites with fewer than four IMM were deemed inconclusive and combined with neutral sites. A Fisher exact test was used to evaluate h_i differences among IMM and RES across strata. A similar evaluation of b_i among these strata was conducted to determine if patterns in h_i were due to differential b_i or hatch rates but only using females for which there was a high level of confidence that all nest attempts were detected. Alpha at 0.10 was used for significance testing due to low sample sizes of IMM in strata.

Early nest initiation and hatch may improve recruitment rates in mallards (Dzus and Clark 1998), so I also evaluated whether RES initiated and hatched nests earlier in the breeding-season than did immigrants, after standardizing initiation and hatch dates of individuals relative to the first known date at each study site (earliest date = 1). Standardized initiation and hatch dates of IMM and RES were compared using a two-sample Kolmogorov-Smirnov test.

5.4 RESULTS

5.4.1 *Natal origin assignments*

DF cross-validation of feather $\delta^{34}\text{S}$, δD , $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ values from pre-fledged ducklings resulted in 81% (112 of 138) successful classification of known-source individuals. Region-specific assignment success was 90%, 84%, and 70% of individuals known to have grown feathers in BOREAL, PARKLAND, and PPR, respectively. Relative to prior distribution of known-source cases, correct classification was 2.5, 2.3, and 2.4 times better than chance for BOREAL, PARKLAND, and PPR regions, respectively. DF estimated that 33, 638, and 54 yearlings captured at study sites originated from BOREAL, PARKLAND, and PPR, respectively. Thus, the subsamples consisted of 87 immigrants and 638 residents. By applying a 0.70 membership probability threshold for analyses, sample sizes were 47 and 328 for immigrants and residents, respectively, and the number of sites where immigrants were present

decreased from 22 to 15. Only results using the most conservative data with high assignment reliability are reported with respect to residency status ($n = 375$).

5.4.2 *Model selection*

The estimate of \hat{c} was ~ 1.0 for all analyses indicating no over-dispersion of the data relative to the most parameterized candidate model. Therefore, I evaluated the rest of the candidate models for each analysis at this scale. Model selection results indicated that the best approximating model for h_i included breeding-pair and wetland densities, along with their interaction, for analyses of all yearling females (Table 5.1A). Other candidate models were not well supported based on ΔAIC_c values ($\Delta AIC_c < 5.0$; Burnham and Anderson 1998). The most parsimonious model for b_i described an effect of wetland density but there was some support for remaining candidate models based on ΔAIC_c values (Table 5.1B). Therefore, model-averaging was used to derive parameter estimates (Table 5.2; Burnham and Anderson 1998).

Relative to residency status, the best approximating model for h_i included breeding-pair and wetland densities with their interaction for analyses of all yearling females (Table 5.3). There was weak evidence of an additive effect of residency status based on ΔAIC_c values. Uncertainty occurred among candidate models based on ΔAIC_c values so model-averaging was used to derive parameter estimates. For bootstrap procedures, I used the model incorporating effects of pair and wetland density and their interaction with an additive effect of residency status.

Table 5.1 Model selection results for hatch rate (A, n = 665) and breeding propensity (B, n = 426) of yearling females monitored at 22 breeding locations in the Canadian aspen parklands during 1993-2000. Model constraints included site breeding-pair (PAIR) and wetland (POND) densities, and their interaction (*). Shown for each model is the number of model parameters (K), Akaike Information Criterion scores adjusted for small sample size (AIC_c), relative AIC_c difference (Δ AIC_c), model likelihood (L_i), and model weight (w_i).

A)

Model	K	AIC _c	Δ AIC _c	L _i	w _i
PAIR POND PAIR*POND	5	489.92	0.00	1.00	1.00
POND	3	512.43	22.51	0.00	0.00
PAIR POND	4	514.41	24.50	0.00	0.00
PAIR	3	518.02	28.10	0.00	0.00

B)

Model	K	AIC _c	Δ AIC _c	L _i	w _i
POND	3	408.14	0.00	1.00	0.48
PAIR POND PAIR*POND	5	408.78	0.64	0.73	0.35
PAIR POND	4	410.16	2.02	0.36	0.17
PAIR	3	411.60	3.46	0.18	0.08

Table 5.2. Logit scale parameter estimates for yearling female mallard breeding propensity (b_i) and hatch rate (h_i) based on model selection results from Tables 5.1A and B.

Parameter	b _i		h _i	
	β^1	SE ¹	β	SE
INTERCEPT	0.573	0.539	-5.506	0.758
PAIR	0.062	0.046	0.489	0.089
POND	0.031	0.014	0.099	0.019
PAIR*POND	-0.005	0.003	-0.012	0.002

¹ Model-averaged values based on relative model weights (w_i) presented in Table 5.2B.

Table 5.3. Top five models evaluating hatch rate of yearling female mallards (n = 375) monitored at 15 sites in the Canadian aspen parklands, 1993-2000, relative to residency status. Model constraints included site breeding-pair (PAIR) and wetland (POND) densities, estimated residency status (RES) and interactions (*). Shown for each model is the number of model parameters (K), Akaike Information Criterion scores adjusted for small sample size (AIC_c), relative AIC_c difference (Δ AIC_c), model likelihood (L_i) and model weight (w_i).

Model	K	AIC _c	Δ AIC _c	L _i	w _i
PAIR POND PAIR*POND	5	361.43	0.00	1.00	0.76
PAIR POND PAIR*POND RES	7	365.08	3.65	0.16	0.12
PAIR POND PAIR*POND RES PAIR*RES	9	365.45	4.03	0.13	0.10
PAIR POND PAIR*POND RES POND*RES	9	369.19	7.76	0.02	0.02
PAIR	3	377.91	16.49	0.00	0.00

5.4.3 Fitness components

Mean values of b_i and h_i for yearling female mallards were 0.82 (95%CI: 0.78 – 0.86) and 0.17 (95% CI: 0.14 – 0.21) based on the most parsimonious models (Tables 5.1A and B). Model-averaged estimates for h_i were 0.20 (95% CI: 0.10 - 0.37) and 0.16 (95% CI: 0.13 - 0.20), for immigrants and residents, respectively. Bootstrap estimates of b_i were 0.83 (95% CI: 0.67 - 0.94) and 0.83 (95% CI: 0.77 - 0.88) and h_i were 0.21 (95% CI: 0.10 - 0.34) and 0.18 (95% CI: 0.13 - 0.22) for, for immigrants and residents, respectively. Distributions of b_i (Kolmogorov-Smirnov test, $D_{\max} = 0.25$, $P < 0.001$) and h_i (Kolmogorov-Smirnov test, $D_{\max} = 0.44$, $P < 0.001$) for immigrants and residents differed in that the frequency of lower and higher values for immigrants exceeded those of residents.

For individuals in which high certainty existed for detecting all nests, median standardized nest initiation day was 14 (range: 1 - 43, n = 30) and 15 (range: 1 - 54, n = 216) and for hatch day was 55 (range: 36 - 75, n = 10) and 65 (range: 37 – 102, n = 65) for immigrants and residents, respectively. Distributions among immigrants and residents were similar for initiation (Kolmogorov-Smirnov test, $D_{\max} = 0.14$, $P = 0.71$) and hatch dates (Kolmogorov-Smirnov test, $D_{\max} = 0.31$, $P = 0.38$). I also explored conditions that might favour immigrants on some sites and residents on others by pooling sites into strata based on which residency status was favoured by $\geq 10\%$. Site-

specific hatch rates indicated that two sites favoured immigrants, two favoured residents, and 11 were similar. Given that females nested, hatch rates differed across pair density classes (i.e., low, medium, and high) for immigrants (Fisher's exact test, Table P = 0.021, $P < 0.06$, $n = 27$) but not for residents (Fisher's exact test, Table P = 0.006, $P = 0.15$, $n = 164$). In summary, the chronology of reproductive effort and success were similar for immigrant and resident yearling females but differed in how hatch rates varied relative to pair density.

5.5 DISCUSSION

5.5.1 *Variation in fitness components*

Yearling female mallard hatch rates showed patterns of both inverse and positive density dependence but the pattern and strength of density dependence was related to local wetland conditions. When wetland abundance was above average, hatch rates had a negative relationship and when below average, a positive relationship with breeding-pair density, respectively (Fig. 5.1). The change in direction of density dependence relative to wetland abundance may explain why local scale patterns in North American mallards have been unclear (Vickery and Nudds 1984). One explanation for a change in density effects includes how wetland conditions might affect both mallard reproductive effort and the location of nests relative to wetlands. Nest predation is the predominant cause of nest failure in mallards (Cowardin et al. 1985) and other birds (Ricklefs 1969) and terrestrial predators often find duck nests incidentally, while en route to visiting wetlands to forage. Wetland abundance positively influences reproductive effort in female mallards (Johnson and Grier 1988) and so nest density may be higher when breeding conditions are "good" and increase the likelihood that predators encounter nests (Larivière and Messier 1998). Hill (1984) found that mallard hatch rates were negatively density dependent because nest predation was positively correlated with nest density, and other investigators have reached similar conclusions (Elmberg et al. 2005). Mack and Clark (2006) found that female mallards with successful nests had fewer wetlands within their home range and they attributed this pattern as a strategy to avoid wetland-associated predators. Thus, when wetland

conditions are poor hatch rates may be positively density dependent because fewer females breed and nest density is lower (Arnold et al. 2007).

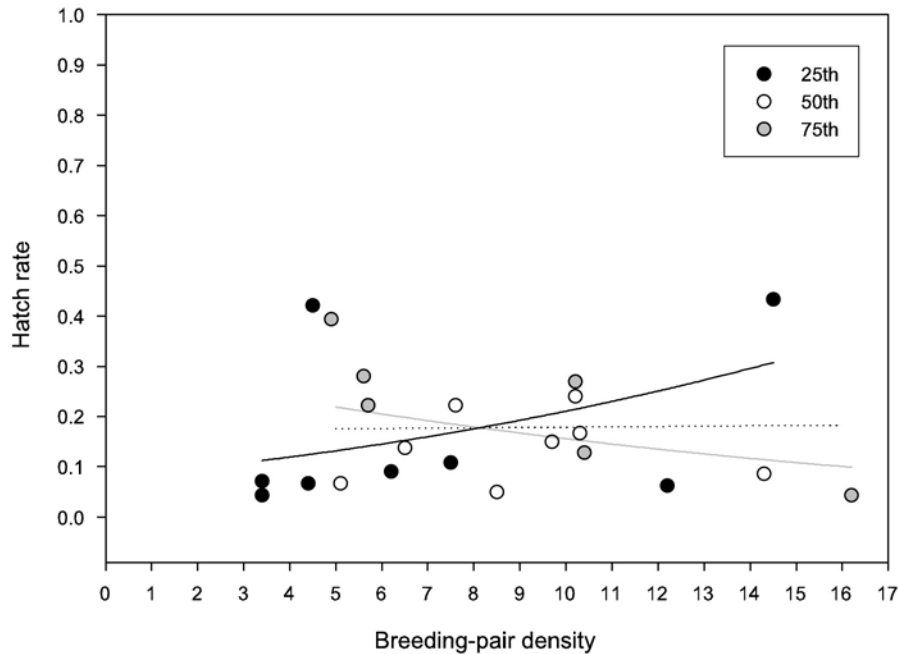


Fig. 5.1. The relationship between hatch rates of yearling female mallards and breeding-pair density (km^2) relative to 25th (black line), 50th (dotted line), and 75th (gray line) quartiles of wetland abundance across 22 locations (circles) in the Canadian aspen parklands, 1993-2000. Parameter estimates for hatch rate are presented in Table 5.2.

Contrary to predictions of the site familiarity hypothesis, resident female mallard yearlings did not consistently have higher hatch rates than did immigrants, nor did residents initiate or hatch nests earlier than immigrants. Immigrant hatch rate was more variable than that of residents, and apparently was associated in part with differences in social factors affecting breeding probability. Immigrant yearlings tended to outperform residents at low breeding-pair density but the reverse was evident at high density (Fig. 5.2). That fitness advantages varied relative to residency status and environmental conditions is consistent with the idea that dispersal is a mechanism

which allows species to mitigate effects of unstable environments. For example, some desert and specialist forest bird species show “nomadic” dispersal strategies whereas others are sedentary, based on whether availability of resources is predictable at fine scales (Gill 1995). Thus, the benefits of site familiarity might be expected to be minimal in nomadic and valuable in sedentary species. Prairie wetlands are a critical resource for mallard productivity (Johnson and Grier 1988) and wetland abundance and distribution can be highly variable across space and time due to local and regional wet-dry cycles (Murkin et al. 2000, Drever et al. 2004). Wet or dry periods may last several years, so fine-scale site familiarity may be most advantageous for mallards when breeding resources are relatively constant and not so when dynamic. To my knowledge, this is the first empirical study showing that an advantage of familiarity from prior natal residence may be conditional on social factors. Other studies comparing fitness of immigrant and resident birds either did not evaluate social factors or found them to be unimportant (Verhulst and van Eck 1996) or concluded that immigrants either do worse than (Verhulst and van Eck 1996, Bensch et al. 1998, Orell et al. 1999, Hansson et al. 2004) or as well as (Pärt 1994) resident songbirds. However, these studies differed in that they measured the fitness of individuals through time in a single population while I measured fitness across a much broader spatial scale.

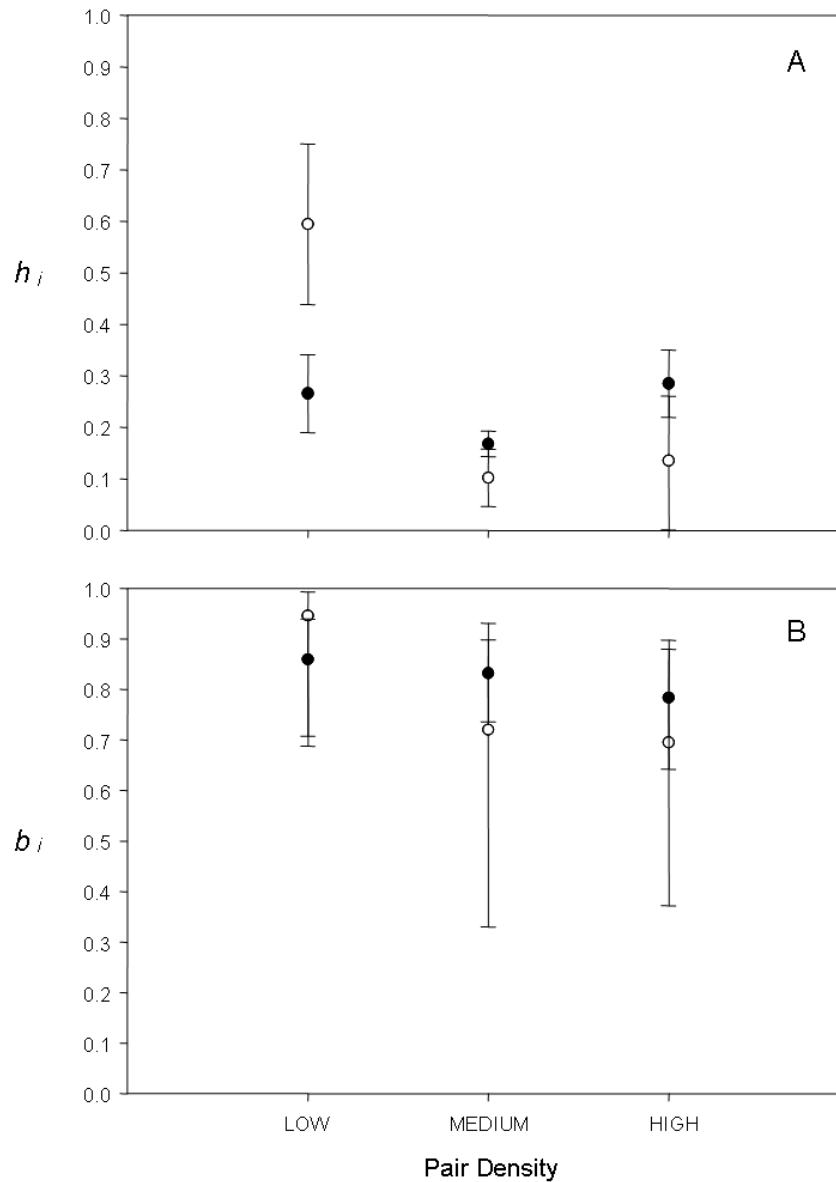


Figure 5.2. (A) Probability estimates (\pm SE) of hatch rate (h_i) and (B) breeding propensity (b_i) relative to breeding pair density (per km²) for yearling female mallards estimated to be immigrants (open circle, $n = 33$) or residents (closed circle, $n = 200$) at breeding locations in the Canadian aspen parklands during 1993-2000. Estimates for h_i and b_i were derived from a sample of females whose nest attempts were confident to be known. Breeding-pair density classes shown are lower 1/3 (LOW), intermediate 1/3 (MEDIUM), and upper 1/3 (HIGH) determined from the range of estimates obtained from May surveys conducted on all study sites.

That the marked population is representative of the yearling mallard populations at the breeding locations is one of several assumptions in this analysis. There is no prior biological expectation that susceptibility to capture in decoy traps would differ between immigrants and residents, so the results from these marked individuals should be relevant to patterns in mallard populations in the Canadian aspen parklands. Another assumption is that residency assignments are reliable. Hebert and Wassenaar (2005a) demonstrated that feather stable isotope values provide highly reliable individual assignments of regional origin at broad spatial scales. Results from the DF cross-validation indicated that correct regional assignment of known-source cases for aspen parkland populations was 2.3 times better than by chance based on prior distributions. Therefore, assignments used here are valid with respect to the spatial scale of this study. Additionally, I further accounted for assignment uncertainty by restricting the analysis to only include females with a >70% posterior assignment probability. Finally, breeding and nesting success rates could be biased if the ability to detect nests differed due to residency status, but there is no *a priori* reason to expect this to be the case since the same search methods and effort were used to locate nests early in laying stage for all radio marked females.

I found that increases in hatch rates for immigrants at low breeding pair density coincided with higher breeding rates. This relationship indicates that the higher hatch rate for immigrants was at least partly due to a greater proclivity to nest and not necessarily because immigrants were choosing better nest sites than residents (Fig. 5.2). In contrast, resident breeding probability was fairly constant with respect to pair density, indicating that when residents were favoured they were probably selecting safer nest sites. That residents were able to obtain safer nest sites than immigrants supports the notion that environmental familiarity is beneficial and is in agreement with most findings in songbirds (Bensch et al. 1998, Hansson et al. 2004) but not all (Orell et al. 1999). Fledging success in ducks can vary considerably due to biotic and abiotic factors (e.g., Krapu et al. 2000, Gendron and Clark 2002) so higher relative fitness due to nest site selection may be lost if offspring do not survive to reproduce. I was unable to directly evaluate whether site familiarity translates into higher fledging success or

future productivity by offspring but evidence from local scale studies of other birds indicates it does (Bensch et al. 1998, Orell et al. 1999).

5.5.2 *Variation in breeding probability*

Increasing wetland conditions had a positive effect on breeding (Table 5.2). This pattern is consistent with those of mallard reproductive effort found at broader spatial scales (Johnson and Grier 1988). Dufour and Clark (2002) suggested that the association between elevated apparent survival rates and poor wetland conditions in younger female mallards could be a product of lower breeding proclivity because nesting females experience lower survival as a consequence of either greater susceptibility to predators (Sargeant et al. 1984) or energetic stress from reneating. However, small differences in model selection AIC_c values (i.e., model selection uncertainty) prevents ruling out that breeding propensity is independent of density (Table 5.1B). Breeding-pair density might negatively influence yearling breeding effort through intraspecific competition where yearling access to breeding resources, such as wetlands or mates, becomes more limited as the local population grows, especially in populations composed of older females. However, whether female ducks show breeding constraint or restraint remains debated (Rohwer 1992, Alisauskas and Ankney 1994, Arnold et al. 2002). Presumably, territorial behaviour makes females more susceptible to capture in decoy traps and so non-breeding yearlings may be under-represented in our data. Breeding probability was more sensitive to local breeding-pair density in immigrant than in resident yearling females. Mallard breeding-pairs establish territories upon arrival at breeding areas and defend them against conspecific intruders, and social dominance favours older females (Dzubin 1952, Anderson and Titman 1992). Under a breeding restraint hypothesis, younger females may be more inclined to breed at lower pair densities because access to breeding space or other resources may be higher due to fewer contests with adult females (Forslund and Pärt 1995). Extending this idea to site familiarity would predict greater immigrant breeding effort at low breeding-pair density relative to resident yearlings as my results indicate (Fig 5.1b). These conditions might occur in areas where prolonged drought has suppressed local productivity and wetlands are suddenly inundated with water from winter precipitation events, phenomena which

occur periodically in prairie systems (Johnson and Grier 1988, Murkin et al. 2000). However, I could not evaluate whether social and habitat conditions were changing because sites were only visited once. Breeding probability among residents was not associated with local breeding-pair densities possibly because of tolerance or assistance by relatives (Weatherhead 1998, Russila et al. 2001) or because familiarity allows residents to avoid competition with unrelated adults or outcompete immigrants (Snell-Rood and Cristol 2005).

There was no evidence that nest initiation or hatch dates varied among resident and immigrants or within these groups across varying environmental conditions. These results are inconsistent with predictions of the site-familiarity hypothesis where residents are expected to obtain higher quality breeding space before immigrants. Failure to detect differences could be due to low immigrant sample sizes for these variables, especially at higher pair densities. Alternatively, residents and immigrant yearlings may arrive at breeding areas at similar times or be subjected to the same physiological constraints which limit when they can nest. Additionally, a lack of breeding experience may inhibit a yearling's ability to predict safe nest sites, especially in variable environments which may differ from natal conditions. However, results comparing the timing of breeding in other birds are mixed despite concluding that residents have higher life-time fitness (see Marr et al. 2002) so other aspects of breeding effort may be more important. While dates related to reproduction did not differ, results showing that immigrants were less likely to nest are consistent site familiarity predictions about differential breeding effort.

Reproductive effort and productivity in dabbling ducks (*Anas spp.*) is positively correlated with increases in annual wetland conditions (Johnson and Grier 1988), a resource which can vary considerably over space and time in prairie habitats (Wilkens et al. 2006). Dufour and Clark (2002) found that survival was higher for younger female mallards when local wetland conditions were poor and attributed this result to breeding avoidance during unfavourable environmental conditions. Although wetland conditions did not contribute significantly to patterns in fitness, I found that differences due to residency status were exaggerated at varying wetland densities (Fig. 5.3). Resident fitness measures were highest when wetland conditions were below normal (Fig. 5.3c).

This pattern suggests that resident females perform better in poorer habitat conditions than do immigrants, possibly because prior experience allows them to better cope with environmental uncertainty in familiar environments.

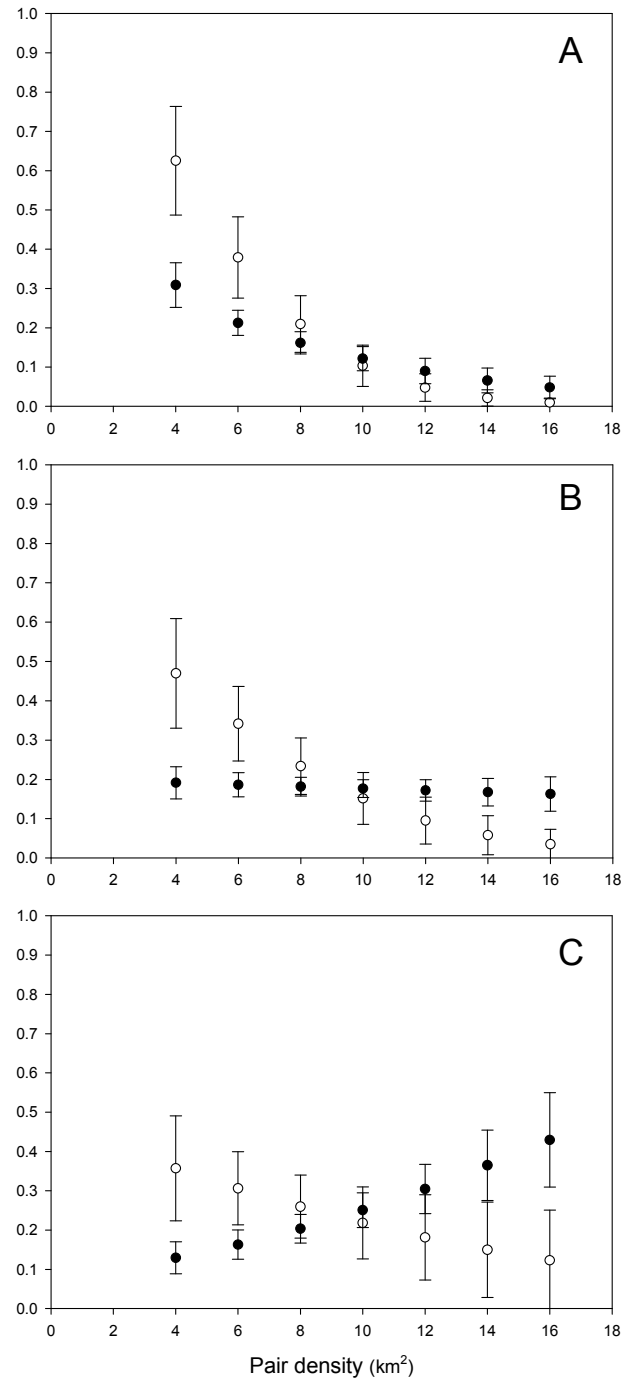


Figure 5.3. Model-averaged hatch probability estimates (\pm SE) versus breeding pair densities at different levels of wetland density for immigrant (open circles, $n = 47$) and resident (closed circles, $n = 328$) yearling female mallards at breeding locations in the Canadian aspen parklands, 1993-2000. Hatch rate estimates are shown at +1 standard deviation (SD; A), mean (B), and -1 SD(C) values of wetland densities (per km²) among study sites.

To my knowledge, I present some of the first estimates of regional immigration in breeding populations using non-banding assessment of origin. Of females with >70.0% probability of regional membership, 12.5% (47 of 375) of yearling females were estimated to have dispersed from other regions and settled at aspen parkland breeding locations. Among immigrants, 26% (12 of 47) were estimated to have natal origins in boreal forest. This rate is similar to that reported for mallards at other aspen parkland sites (Coulton and Clark 2008) and suggests that the boreal region may be more important to recruitment than previously believed. However, 74% of immigrants (35 of 47) were estimated to have natal origins in the U.S. prairie pothole region, an area believed to be highly productive for waterfowl due to wetland and grassland conservation policy (Reynolds et al. 2001, Reynolds et al. 2006). Presumably, immigrants settled at aspen parkland sites because environmental conditions were more favourable for reproductive success than in southern areas. However, how and why environmental cues influence immigration rates warrants further investigation (Chapter 4).

LITERATURE CITED

- Allee, W. C. 1951. The social life of animals. Beacon Press, Boston, MA.
- Amundson, R., A.T. Austin, E.A.G. Schuur, K. Yoo, V. Matzek, C. Kendall, A. Uebersax, D. Brenner, and W.T. Baisden. 2003. Global patterns of the isotopic composition of soil and plant nitrogen. *Global Biogeochemical Cycles* 17:1031, doi:10.1029/2002GB001903.
- Anderson, M. G., J. M. Rhymer, and F. C. Rohwer. 1992. Philopatry, dispersal and the genetic structure of waterfowl populations. Pages 235-395 *in* Ecology and management of breeding waterfowl, (B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, MN.
- Anderson, M. G., R. D. Titman. 1992. Spacing patterns. Pages 251-289 *in* Ecology and management of breeding waterfowl, (B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, MN.
- Arnold, T. W., M. D. Sorenson, and J. J. Rotella. 1993. Relative success of overwater and upland mallard nests in southwestern Manitoba. *Journal of Wildlife Management* 57:578-581.
- Arnold, T. W., and R. G. Clark. 1996. Survival and philopatry of female dabbling ducks in southcentral Saskatchewan. *Journal of Wildlife Management* 60:560-568.
- Arnold, T. W., M. G. Anderson, M. D. Sorenson, and R. B. Emery. 2002. Survival and philopatry of female redheads breeding in Southwestern Manitoba. *Journal of Wildlife Management* 66:162-169.

- Arnold T. W., L. M. Craig-Moore, L. M. Armstrong, D. W. Howerter, J. H. Devries, B. L. Joynt, R. B. Emery, and M. G. Anderson. 2007. Waterfowl use of dense nesting cover in the Canadian Parklands. *Journal of Wildlife Management* 71: 2542-2549.
- Artmann, M. J., I. J. Ball, and T. W. Arnold. 2001. Influence of perennial upland cover on occupancy of nesting structures by mallards in northeastern North Dakota. *Wildlife Society Bulletin* 29:232-238.
- Batt, B. D. J., M. G. Anderson, C. D. Anderson, and F. D. Caswell. 1989. The use of prairie potholes by North American ducks. Pp. 204-227 in *Northern prairie wetlands* (van der Valk, A., eds.). Iowa State University Press, Ames, IA.
- Bensch, S., D. Hasselquist, B. Neilsen, B. Hansson. 1998. Higher fitness for philopatric than immigrant males in a semi-isolated population of great reed warblers. *Evolution* 52:877-883.
- Bellrose, F. C. 1980. *Ducks geese and swans of North America*. Stackpole Books, Harrisburg, PA.
- Bishop, R. A., and R. Barratt. 1970. Use of artificial nest baskets by mallards. *Journal of Wildlife Management* 34:734-738.
- Blais, S., M. Guillemain, B. Durant, H. Fritz, and N. Guillon. 2001. Growth and plumage development of Pintail ducklings. *Wildfowl* 52: 69-86.
- Blums, P. E., J. B. Davis, S. E. Stephens, A. Mednis, and D. M. Richardson. 1999. Evaluation of a plasticine-filled leg band for day-old ducklings. *Journal of Wildlife Management* 63:656-663.

- Blums, P., J. D. Nichols, J. E. Hines, M. S. Lindberg, and A. Mednis. 2003. Estimating natal dispersal movement rates of female European ducks with multistate modeling. *Journal of Animal Ecology* 72:1027-1042.
- Boughton, D. A. 1999. Empirical evidence for complex source-sink dynamics with alternative states in a butterfly metapopulation. *Ecology* 80:2727-2739.
- Bowen, G. J., L. I. Wassenaar, and K. A. Hobson. 2005. Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia* 143:337-348.
- Breiman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and regression trees. Wadsworth and Brooks/Cole Advanced Books and Software, Monterey, CA.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: immigration or extinction. *Ecology* 58:445-449.
- Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173-1187.
- Burger, G. V., and C. G. Webster. 1964. Instant nesting habitat. Pages 655-666 in *Waterfowl tomorrow* (J. P. Liduska and A. L. Nelson, Eds.). Bureau of Sport Fisheries and Wildlife, Washington, DC.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer-Verlag, New York, NY.
- Caudill, C. C. 2003. Empirical evidence for nonselective and a source-sink dynamic in a mayfly metapopulation. *Ecology* 84:2119-2132.

- Calverley, B. K., and D. A. Boag. 1977. Reproductive potential in parkland- and arctic-nesting populations of mallards and pintails (*Anatidae*). *Canadian Journal of Zoology* 55:1242-1250.
- Chouinard, M. D., R. M. Kaminski, P.D. Gerard, and S. J. Dinsmore. 2005. Experimental evaluation of duck nesting structures in Prairie Parkland Canada. *Wildlife Society Bulletin* 33:321-329.
- Clark, R. G., and D. Shutler. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology* 80:272-287.
- Clark, R. G., K. A. Hobson, J. D. Nichols, and S. Bearhop. 2004. Avian dispersal and demography: Scaling up to the landscape and beyond. *Condor* 106:717-719.
- Clark, R. G., K. A. Hobson, L. I. Wassenaar. 2006. Geographic variation in the isotopic (δD , $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) composition of feathers and claws from lesser scaup and northern pintail: implications for studies of migratory connectivity. *Canadian Journal of Zoology* 84:1395-1401.
- Clobert, J.C., E. Danchin, A. A. Dhondt, and J. D. Nichols. 2001. *Dispersal*. Oxford University Press, Inc., NY.
- Cooch, E. G., and G. C. White. 2007. Program MARK: A Gentle Introduction, 6th edition. [Online.] Available at: <http://www.phidot.org/software/mark/docs/book/>.
- Cormie, A. B., H. P. Schwarcz, and J. Gray. 1994. Relation between hydrogen isotopic ratios of bone collagen and rain. *Geochim Cosmochim Acta* 58:377-391.
- Coulton, D. W., and R. G. Clark. 2008. An integrated capture-recapture isotopic approach to modeling sources of population rescue. *Auk* 125:923-931.

- Cowardin, L. M., D. S. Gilmer, and C. W. Shaiffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. *Wildlife Monographs* 92:5-37.
- Cowardin, L. M. and R. J. Blohm. 1992. Breeding population inventories and measures of recruitment. Pages 423-445 *in* Ecology and management of breeding waterfowl, (B.D. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu, Eds.). University of Minnesota Press, Minneapolis, MN.
- Craig, H. L. I. Gordon, and Y. Horibe. 1963. Isotopic exchange effects in evaporation of water .1. low temperature experimental results. *Journal of Geophysical Research* 68:5079.
- Cryan, P. M., M. A. Bogan, R. O. Rye, G. P. Landis, and C. L. Kester. 2004. Stable hydrogen analysis of bat hair as evidence for seasonal molt and long-distance migration. *Journal of Mammalogy* 85: 995-1001.
- Cunjak, R. A., J.-M. Roussel, M. A. Gray, J. P. Dietrich, D. F. Cartwright, K. R. Munkittrik, and T. D. Jardine. 2005. Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. *Oecologia* 144:636-646.
- Dansgaard, W. G. Nief, and G. Roth. 1960. Isotopic distribution in a Greenland iceberg. *Nature* 185:232.
- Devries, J. H., J. J. Citta, M. S. Lindberg, D. W. Howerter, and M. G. Anderson. 2003. Breeding-season survival of mallard females in the Prairie Pothole Region of Canada. *Journal of Wildlife Management* 67:551-563.
- Dieckmann, U., B. O'Hara, and W. Weisser. 1999. The evolutionary ecology of dispersal. *Trends in Ecology and Evolution* 14:88-90.

- Doherty, P. F., Jr., J. D. Nichols, J. Tautin, J. F. Voelzer, G. W. Smith, D. S. Benning, V. R. Bentley, J. K. Bidwell, K. S. Bollinger, A. R. Brazda, E. K. Buelna, J. R. Goldsberry, R. J. King, F. H. Roetker, J. W. Solberg, P. P. Thorpe, and J. S. Wortham. 2002. Sources of variation in breeding-ground fidelity of mallards. *Behavioral Ecology* 13:543-550.
- Doligez, B., T. Pärt, E. Danchin, J. Clobert, and L. Gustaffson. 2004. Availability and use of public information and conspecific density for settlement decisions in the collard flycatcher. *Journal of Animal Ecology* 73:75-87.
- Doty, H. A. 1979. Duck nest structure evaluation in prairie wetlands. *Journal of Wildlife Management* 43:976-979.
- Doty, H. A., F. B. Lee, and A. D. Kruse. 1975. Use of elevated nest baskets by ducks. *Wildlife Society Bulletin* 3:68-73.
- Drever, M. C., A. Wins-Purdy, and T. D. Nudds. 2004. Decline of ducks revisited: Relationships with predators and wetlands in dynamic prairie environments. *Auk* 121:497-508.
- Dufour, K. W. and R. G. Clark. 2002. Differential survival of yearling and adult female mallards and its relation to breeding habitat conditions. *Condor* 104:297-308.
- Dzubin, A. 1952. Waterfowl production and behaviour study in the Minnedosa pothole district of Manitoba. Pages 71-75 *in* Waterfowl populations and breeding conditions-summer 1952. U.S. Fish and Wildlife Service, Report 21.
- Dzubin, A. 1957. Pairing display and spring and summer flights of the mallard. *Blue Jay* 15:10-13.

- Dzubin, A. 1969. Assessing breeding populations of ducks by ground counts. Canadian Wildlife Service Report Series 6:178–230.
- Dzubin, A., and J. B. Gollop. 1972. Aspects of Mallard breeding ecology in Canadian parkland and grassland. Pages 113-152 in Population ecology of migratory birds (R. I. Smith, J. R. Palmer, and T. S. Baskett, Eds.). United States Fish and Wildlife Service Wildlife Report No. 2, Washington, DC.
- Dzus, E. H. and R. G. Clark. 1998. Brood survival and recruitment of mallards in relation to wetland density and hatching date. Auk 115:311-318.
- Ecological Stratification Working Group. 1995. A national ecological framework for Canada. Agriculture and Agri-Food Canada, Research Branch Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Hull, PQ, CA.
- Elmberg, J. 2003. Density dependent breeding success in mallards *Anas platyrhynchos* on a eutrophic lake. Wildlife Biology 9:67-73.
- Elmberg, J., G. Gunnarsson, H. Pöysä, K. Sjöberg, and P. Nummi. 2005. Within-season sequential density dependence regulates breeding success in mallards *Anas platyrhynchos*. Oikos 108:582-590.
- Emery, R. B., D. W. Howerter, L. M. Armstrong, M. G. Anderson, J. H. Devries, and B. L. Joynt. 2005. Seasonal variation in waterfowl nesting success and its relation to cover management in the Canadian Prairies. Journal of Wildlife Management 69:1181-1193.
- Etterson, M.A. 2003. Conspecific attraction in loggerhead shrikes: implications for habitat conservation and reintroduction. Biological Conservation 114:199-205.

- Fletcher, R. J., Jr. 2006. Emergent properties of conspecific attraction in fragmented landscapes. *American Naturalist* 168:207-219.
- Fletcher, R. J., Jr. 2007. Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology* 76:598-606.
- Forslund, P., and Pärt. T. 1995. Age and reproduction in birds-hypotheses and tests. *Trends in Ecology and Evolution* 10:374–378.
- Fretwell, S. D., and H. L. Lucas, Jr. 1970. On the territorial behavior and other factors influencing habitat distribution in birds: I. Theoretical development. *Acta Biotheoretica* 19:17-36.
- Gendron, M., and R. G. Clark. 2002. Survival of gadwall and mallard ducklings in southcentral Saskatchewan. *Journal of Wildlife Management* 66:170-180.
- Gill, F. B. 1995. *Ornithology*, 2nd Edition. W. H. Freeman Company, NY.
- Graves, G.R., C.S. Romanek, and A.R. Navarro. 2002. Stable isotope signature of philopatry and dispersal in a migratory songbird. *Proceedings of the National Academy of Sciences* 99:8096–8100.
- Green, R. E. 1989. Transformation of crude proportions of nests that are successful for comparison with Mayfield estimates of nest success. *Ibis* 131:305-306.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140-1162.
- Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1-21.

- Greenwood, R. J., A. B. Sargeant, D. H. Johnson, L. M. Cowardin, and T. L. Shaffer. 1995. Factors associated with duck nest success in the Prairie Pothole Region of Canada. *Wildlife Monographs* 128:1-57.
- Hanski, I. 2001. Population dynamic consequences of dispersal in local populations and metapopulations. Pages 283-289 in *Dispersal*, (Clobert, J.C., E. Danchin, A. A. Dhondt, and J. D. Nichols, Eds.). Oxford University Press, Inc., NY.
- Hansson, B., S. Bensch, and D. Hasselquist. 2004. Life time fitness of short- and long-distance dispersing great reed warblers. *Evolution* 58:2546-2557.
- Haworth, M. and K. F. Higgins. 1993. Waterfowl use and production from nesting baskets and bales in South Dakota wetlands. *Prairie Naturalist* 25:149-160.
- Hazler, K. R. 2004. Mayfield logistic regression: a practical approach for an analysis of nest survival. *Auk* 121:707-716.
- Hebert, C. E. and L. I. Wassenaar. 2001. Stable nitrogen isotopes in waterfowl feathers reflect agricultural land use in western Canada. *Environmental Science & Technology* 35:3482-3487.
- Hebert, C. E. and L. I. Wassenaar. 2005a. Feather stable isotope in western North American waterfowl: spatial patterns, underlying factors, and management applications. *Wildlife Society Bulletin* 33:92-102.
- Hebert, C. E. and L. I. Wassenaar. 2005b. Stable isotopes provide evidence for poor northern pintail production on the Canadian prairies. *Journal of Wildlife Management* 69:101-109.
- Heitmeyer, M. E. 1987. The prebasic moult and basic plumage of female mallards (*Anas platyrhynchos*). *Canadian Journal of Zoology* 65:2248-2261.

- Hestbeck J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* 72:523-533.
- Hill, D. A. 1984. Population regulation in the mallard (*Anas platyrhynchos*). *Journal of Animal Ecology* 53:191-202.
- Hines, J. E., and J. D. Nichols. 2002. Investigations of potential bias in the estimation of λ using Pradel's (1996) model for capture-recapture data. *Journal of Applied Statistics* 29:573-587.
- Hobson, K. A. 1999. Stable-carbon and nitrogen isotope ratios of songbird feathers grown in two terrestrial biomes: implications for evaluating trophic relationships and breeding origins. *Condor* 101:799-805.
- Hobson, K. A. 2002. Incredible journeys. *Science* 295:981-983.
- Hobson, K. A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions* 11:157-164.
- Hobson, K. A. 2008. Applying isotopic methods to tracking animal movements. Pages 45-79 in, *Tracking animal migration with stable isotopes*, Hobson, K. A. and Wassenaar, L. I. (eds.). Elsevier Inc., New York, NY.
- Hobson, K. A., and L. I. Wassenaar. 1997. Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* 109:142-148.

- Hobson, K. A., L. I. Wassenaar, and E. Bayne. 2004. Using isotopic variance to detect long-distance dispersal and philopatry in birds: an example with ovenbirds and American redstarts. *Condor* 106:732-743.
- Hobson, KA, L. I. Wassenaar, B. Milá, I. Lovette, C. Dingle, T. B. Smith. 2003. Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. *Oecologia* 136:302–308.
- Hobson, K. A., S. Van Wilgenburg, L. I. Wassenaar, H. Hands, W. P. Johnson, M. O’Meilia, and P. Taylor. 2006. Using stable hydrogen isotope analysis of feathers to delineate origins of harvested sandhill cranes in the central flyway of North America. *Waterbirds* 29:137-147.
- Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analysis of the life cycle of midcontinent mallards. *Journal of Wildlife Management* 66(3):883-898.
- Hohman, W. L., C. D. Ankney, and D. H. Gordon. 1992. Ecology and management of postbreeding waterfowl. Pages 128-189 *in* Ecology and management of breeding waterfowl, (B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, MN.
- Howerter, D. W., B. L. Joynt, and R. B. Emery. 1997. Effects on nasal discs on nesting by mallards. *Journal of Field Ornithology* 68:1-6.
- Ims, R. A., and D. Ø. Hjernmann. 2001. Condition-dependent dispersal. Pages 201-216 *in* Dispersal (J. Clobert, E. Danchin, A. Dhondt, and J. Nichols, Eds.). Oxford University Press, Inc., NY.
- Institute for Wetland and Waterfowl Research, Ducks Unlimited Canada. 1999. PHJV Habitat Program Assessment; Preliminary Results from the 1998 Study Sites.

Interim Report, in Alberta, Saskatchewan and Manitoba. October 8, 1999.
Stonewall, Manitoba.

Jeanson R, and D.L. Deneubourg. 2007. Conspecific attraction and shelter selection in gregarious insects. *American Naturalist* 170:47-58.

Jehle R., G. A. Wilson, J. W. Arntzen, and T. Burke. 2005. Contemporary gene flow and the spatio-temporal genetic structure of subdivided newt populations (*Triturus cristatus*, *T-marmoratus*). *Journal of Evolutionary Biology* 18:619-628.

Johnson, D. H. and J. W. Grier. 1988. Determinants of breeding distributions of ducks. *Wildlife Monographs* 100:1-37.

Johnson, D. H., J. D. Nichols, and M. D. Schwartz. 1992. Population dynamics of breeding waterfowl. Pages 446-485 in *Ecology and management of breeding waterfowl*, (B.D. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu, Eds.). University of Minnesota Press, MN.

Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using mammals and birds. *Annual Review of Ecology and Systematics* 21:449-480.

Julliard, R., P. Perret, and J. Blondel. 1996. Reproductive strategies of philopatric and immigrant blue tits. *Acta Oecologia* 17:487-501.

Kaminski, R. M., and E. A. Gluesing. 1987. Density- and habitat-related recruitment in mallards. *Journal of Wildlife Management* 51:141-148.

Kelly, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78:1-27.

- Klett, A. T., H. F. Duebbert, S. A. Fanes, and K. F. Higgins. 1986. Techniques for studying nest success of ducks in upland habitats in the Prairie Pothole Region. U.S. Fish and Wildlife Service Resource Publication 158, Laurel, MD.
- Klett, A. T., T. L. Shaffer, and D. H. Johnson. 1988. Duck nest success in the Prairie Pothole Region. *Journal of Wildlife Management* 52:431-440.
- Krapu, G. L., R. J. Greenwood, C. P. Dwyer, K. M. Kraft, and L. M. Cowardin. 1997. Wetland use, settling patterns, and recruitment in mallards. *Journal of Wildlife Management* 61:736-746.
- Krapu, G. L., D. H. Johnson, and C. W. Dane. 1979. Age determination of mallards. *Journal of Wildlife Management* 43:384-393.
- Krapu, G. L., A. T. Klett, and D. G. Jorde. 1983. The effect of variable spring water conditions on mallard reproduction. *Auk* 100:689-698.
- Krapu, G. L., P. J. Pietz, D. A. Brandt, and R. R. Cox. 2000. Factors limiting mallard brood survival in prairie pothole landscapes. *Journal of Wildlife Management* 64:553-561.
- Krebs, C. J. 1972. *Ecology*. Harper and Row, NY.
- Kristan, W. B. 2003. The role of habitat selection behavior in population dynamics: source-sink systems and ecological traps. *Oikos* 103:457-468.
- Langin, K. M., M. W. Reudink, P. P. Marra, D. R. Norris, T. K. Kyser, and L. M. Ratcliffe. 2007. Hydrogen isotopic variation in migratory bird tissue of known origin: implications for geographic assignment. *Oecologia* 152:449-457.

- Lariviere, S., and F. Messier. 1998. Effect of density and nearest neighbours on simulated waterfowl nests: can predators recognize high-density nesting patches? *Oikos* 83:12-20.
- Lecchini D, S. Planes, and R. Glazin. 2007. The influence of habitat characteristics and conspecifics on attraction and survival of coral reef fish juveniles. *Journal of Experimental Marine Biology and Ecology* 341:85-90.
- Littel, R. C., W. W. Stroup, and R. J. Freund. 2002. SAS® for Linear models, 4th Edition, Cary NC, SAS Institute, Inc.
- Loh, W.-Y., and Y.-S. Shih. 1997 Split selection methods for classification trees. *Statistica Sinica* 7:815-840.
- Lokemoen, J. T., and D. E. Sharp. 1985. Assessment of nasal marker materials and designs used on dabbling ducks. *Wildlife Society Bulletin* 13:53-56.
- Lokemoen, J. T., and R. O. Woodward. 1992. Nesting waterfowl and water birds on natural islands in the Dakotas and Montana. *Wildlife Society Bulletin* 20:163-171.
- Lott, C. A., and J. P. Smith. 2006. A geographic-information-system approach to estimating the origin of migratory raptors in North America using stable isotope ratios in feathers. *Auk* 123:822-835.
- Lynch, J. J., C. D. Evans, and V. C. Conover. 1963. Inventory of waterfowl environments of prairie Canada. *Transactions of the 28th North American Wildlife Conference*:93-108.
- MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.

- Mack, G. G., and R. G. Clark. 2006. Home-range characteristics, age, body size, and breeding performance of female mallards (*Anas platyrhynchos*). *Auk* 123:467-474.
- Majewski, P. and P. Beszterda. 1990. Influence of nesting success on female mallard homing. *Journal of Wildlife Management* 54:549-462.
- Marr, A. B. L. F. Keller, and P. Arcese. 2002. Heterosis and outbreeding depression in descendants on natural immigrants to an inbred population of song sparrows. *Evolution* 56:131-142.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird using stable-carbon isotopes. *Science* 282:1884-1886.
- Marshall, J. D., J. R. Brookes, and K. Lajtha. 2007. Sources of variation in stable isotopic composition of plants. Pages 22-50 *in*, *Stable Isotopes in Ecology and Environmental Sciences* 2nd edition, (K. Lajtha, and R. Michener, eds.). Blackwell publishing, Oxford, U.K.
- Martin, K., P. B. Stacey, and C. E. Braun. 2000. Recruitment, dispersal, and demographic rescue in spatially-structured white-tail ptarmigan populations. *Condor* 102:503-516.
- McKinnon, D. T., and D. C. Duncan. 1999. Effectiveness of dense nesting cover for increasing duck production in Saskatchewan. *Journal of Wildlife Management* 63:382-389.
- Meehan, T. D., R. N. Rosenfield, V. N. Atudorei, J. Bielefeldt, L. J. Rosenfield, A. C. Stewart, W. E. Stout, and M. A. Bozek. 2003. Variation in hydrogen stable-isotope ratios between adult and nestling Cooper's hawks. *Condor* 105:567-572.

- Meehan, T. D., J. T. Giermakowski, and P. M. Cryan. 2004. GIS-based model of stable hydrogen isotope ratios in North American growing-season precipitation for use in animal movement studies. *Isotopes in Environmental and Health Studies* 40:291-300.
- Miller, M. W. 2000. Modelling annual mallard production in the Prairie-parkland region. *Journal of Wildlife Management* 64:561-575.
- Mitsch, W. J., and J. G. Gosselink. 2000. *Wetlands*, 3rd edition. John Wiley and Sons, Inc., NY.
- Murkin, H. R., A. G. van der Valk, and W. R. Clark. 2000. *Prairie wetland ecology*. Iowa State University Press, IA.
- Nichols, J. D., J. E. Hines, J.-D. Lebreton, and R. Pradel. 2000. Estimations of contributions to population growth: a reverse-time capture-recapture approach. *Ecology* 81:3362-3376.
- Nichols, J. D., R. S. Pospahala, and J. E. Hines. 1982. Breeding-ground habitat conditions and the survival of mallards. *Journal of Wildlife Management* 46:80-87.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences* 271:59-62.
- Orell, M., K. Lahti, K. Koivula, S. Rytkönen, and P. Welling. 1999. Immigration and gene flow in a northern willow tit (*Parus montanus*) population. *Journal of Evolutionary Biology* 12:283-295.

- Pärt, T. 1994. Male philopatry confers a mating advantage in the migratory collard flycatcher, *Ficedula albicollis*. *Animal Behaviour* 48:401-409.
- Peng, H., B. Mayer, S. Harris, and H. R. Krouse. 2004. A 10-yr record of stable isotope ratios of hydrogen and oxygen in precipitation at Calgary, Alberta, Canada. *Tellus* 56B:147-159.
- Powell, L. A. 2004. A multistate capture-recapture model using *a posteriori* classification to enhance movement rates. *Condor* 106:761-767.
- Pöysä, H., J. Elmberg, K. Sjöberg, and P. Nummi. 1998. Habitat selection rules in breeding mallards (*Anas platyrhynchos*): a test of two competing hypotheses. *Oecologia* 114:283-287.
- Pradel, R. 1996. Utilization of capture-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703-709.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Reinecker, W. C. 1990. Harvest distribution and survival of mallards banded in California, 1948-1982. *California Fish & Game* 76:14-30.
- Reynolds, R. E., R. J. Blohm, J. D. Nichols, and J. E. Hines. 1995. Spring-summer survival rates of yearling versus adult mallard females. *Journal of Wildlife Management* 59:691-696.
- Reynolds, R. E., T. L. Shaffer, R. W. Renner, W. E. Newton, and B. D.J. Batt. 2001. Impact of the Conservation Reserve Program on duck recruitment in the U.S. Prairie Pothole Region. *Journal of Wildlife Management*, 65:765-780.

- Reynolds, R. E., T. L. Shaffer, C. R. Loesch, and R. R. Cox, Jr. 2006. The Farm Bill and duck production in the Prairie Pothole Region: increasing the benefits. *Wildlife Society Bulletin* 34:963-974.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9:1-48.
- Royale, J. A., and D. R. Rubenstein. 2004. The role of species abundance in determining breeding origins of migratory birds with stable isotopes. *Ecological Applications* 14:1780-1788.
- Rozanski, K., L. Araguás-Araguás, and R. Gonfiantini. 1992. Relation between long-term trends in oxygen-18 isotope composition of precipitation and climate. *Science* 258:981-985.
- Rubenstein, D. R., C. P. Chamberlain, R. T. Holmes, M. P. Ayers, J. R. Waldbauer, G.R. Graves, and N. C. Tuross. 2002. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. *Science* 295:1062-1065.
- Rubenstein, D. R., and K. A. Hobson. 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution* 19:256-263.
- Russila, V., H. Pöysä, and R. Runko. 2001. Costs and benefits of female-biased natal philopatry in the common goldeneye. *Behavioral Ecology* 12:686-690.
- SAS Institute, Inc. 2008. SAS OnlineDoc[®] 9.1.3. Cary, NC.
- Sargeant, A. B., S. H. Allen, and R. T. Eberhardt. 1984. Red fox predation on breeding ducks in midcontinent North-America. *Wildlife Monographs* 89:1-41.

- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17:474-480.
- Schiegl, W. E., and J. C. Vogel. 1970. Deuterium content of organic matter. *Earth and planetary science letters* 7:307-313.
- Sellers, R. A. 1973. Mallard releases in understocked prairie pothole habitat. *Journal of Wildlife Management* 37:10-22.
- Sharp, D. E. and J. T. Lokemoen. 1987. A decoy trap for breeding-season mallards in North Dakota. *Journal of Wildlife Management* 51:711-715.
- Sheafer, S. E. 1998. Recruitment models for mallards in eastern North America. *Auk* 115: 998-997.
- Snell-Rood, E. C., and D. A. Cristol. 2005. Prior residence influences contest outcome in flocks of non-breeding birds. *Ethology* 111:441-454.
- Stacey, P. B., and M. Taper. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2:18-29.
- Saether, B-E., M. Lillegård, V. Grøtan, M. C. Drever, S. Engen, T. D. Nudds, and K. M. Prodrutzny. 2008. Geographical gradients in the population dynamics of North American prairie ducks. *Journal of Animal Ecology* 77:869-882.
- Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. *American Naturalist* 131:329-347.
- Stamps, J. A. 1991. The effect of conspecifics on habitat selection in territorial species. *Behavioral Ecology and Sociobiology* 28:29-36.

- Stamps, J. A. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. Pages 230-242 in *Dispersal* (J. Clobert, E. Danchin, A. Dhondt, and J. Nichols, Eds) Oxford University Press, NY.
- Stamps, J. A., and R. R. Swaisgood. 2007. Some place like home: Experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* 102:392-409.
- StatSoft. 2000. Statistica's user's guide. StatSoft Inc., Tulsa, OK.
- Studds, C. E., T. K. Kyser, and P. P. Marra. 2008. Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory song bird. *Proceedings of the National Academy of Sciences* 105:2929-2933.
- Suits, N.S., A.S. Denning, J.A. Berry, C.J. Still, J. Kaduk, J.B. Miller, and I.T. Baker. 2005. Simulation of carbon isotope discrimination of the terrestrial biosphere, *Global Biogeochemical Cycles* 19 GB1017, doi:10.1029/2003GB002141.
- Szymanski, M. L., A. D. Afton, and K. A. Hobson. 2007. Use of stable isotope methodology to determine natal origin of mallards at a fine scale within the upper midwest. *Journal of Wildlife Management* 71:1317-1324.
- van der Kamp, G., and M. Hayashi. *In press*. Groundwater-wetland ecosystem interaction in the semiarid glaciated plains of North America. *Hydrogeology Journal*.
- Verhulst, S., and H. M. van Eck. 1996. Gene flow and immigration rate in an island population of great tits. *Journal of Evolutionary Biology* 9:771-782.
- Vickery, W. L., and T. D. Nudds. 1984. Detection of density-dependent effects in annual duck censuses. *Ecology* 65:96-104.

- Viljugrein, H., N. C. Stenseth, G. W. Smith, and G. H. Steinbakk. 2005. Density dependence in North American ducks. *Ecology* 86:245-254.
- Wagner, R. H. 1997. Hidden leks: sexual selection and the clumping of avian territories. Pages 123-145 in *Extra-pair mating tactics in birds*. Ornithological Monographs American Ornithologist's Union, Washington, DC.
- Watkinson, A. R., and W. J. Sutherland. 1995. Sources, sinks, and pseudo-sinks. *Journal of Animal Ecology* 64:126-130.
- Wassenaar, L. I., and K. A. Hobson. 1998. Natal origins of migratory monarch butterflies at wintering colonies in Mexico: New isotopic evidence. *Proceedings of the National Academy of Sciences* 99:15436-15439.
- Wassenaar, L. I., and K. A. Hobson. 2000. Stable-carbon and hydrogen isotope ratios reveal breeding origins of red-winged blackbirds. *Ecological Applications* 10:911-916.
- Wassenaar, L. I., and K. A. Hobson. 2003. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotope in Environmental and Health Studies* 39: 211-217.
- Wassenaar, L. I., and K. A. Hobson. 2006. Stable-hydrogen isotope heterogeneity in keratinous materials: mass spectrometry and migratory wildlife tissue subsampling strategies. *Rapid communications in mass spectrometry* 20:2505-2510.
- Weatherhead, P. J. 1998. Natal philopatry and local resource competition in the common goldeneye. *Journal of Avian Biology* 29:321-322.

- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* 17:76-83.
- Weller, M.W. 1957. An automatic nest-trap for waterfowl. *Journal of Wildlife Management* 21:456-458.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120-139.
- Wilkins, K. A., M. C. Otto, and M. D. Koneff. 2006. Trends in duck breeding populations, 1955-2006. Administrative Report, U. S. Fish and Wildlife Service, Division of Migratory Bird Management, Laurel, MD.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and Management of Animal Populations*. Academic Press, CA.
- Winkler, D. W., P. H. Wrege, P. E. Allen, T. L. Kast, P. Senesac, M. W. Wasson, P. J. Sullivan. 2005. The natal dispersal of Tree swallows in a continuous mainland environment. *Journal of Animal Ecology* 74:1080-1090.
- Withey, J. C., and J. M. Marzluff. 2005. Dispersal by juvenile American crows (*Corvus brachyrhynchos*) influences population dynamics across a gradient of urbanization. *Auk* 122:205-221.
- Woo, M-K., and R. D. Rowsell. 1993. Hydrology of a prairie slough. *Journal of Hydrology* 146:175-207.

- Wunder, M. B., C. L. Kester, F. L. Knopf, and R. O. Rye. 2005. A test of geographic assignment using isotope tracers in feathers of known origin. *Oecologia* 144:607-617.
- Wunder, M. B., and D. R. Norris. 2008. Improved estimates of certainty in stable-isotope-based methods for tracking migratory animals. *Ecological Applications* 18:549-559.
- Yerkes, T. 1997. A trap for ducks using artificial nest structures. *Journal of Field Ornithology* 68:147-149.
- Ziegler, H. 1989. Hydrogen isotope fractionation in plant tissues. *In*, Stable isotopes in ecological research, (Rundel P.W., Ehleringer J.R., Nagy K.A., Eds.). Springer Berlin Heidelberg New York, NY.

APPENDIX A. BROAD AND LOCAL-SCALE PATTERNS OF TEMPORAL VARIATION IN FEATHER DEUTERIUM VALUES OF WATERBIRDS

A1.1 ABSTRACT

Strong spatial structure in deuterium (δD) values in mean growing-season precipitation (δD_p) and consumer tissues has led to advances in understanding continental-scale patterns of migration in many taxa in North America. However, limits of resolution at finer spatial scales due to among-individual variance at specific sampling locations, and spatiotemporal variation in δD_p , remain poorly quantified and have not been fully examined in wetland-associated birds. At scales >500 km, we found that annual differences accounted for 0-45% of variation in feather deuterium (δD_f) values of wild hatching-year mallards (*Anas platyrhynchos*) captured in late-summer at sites in four Canadian ecoregions. At scales <50 km, we found that among- and within-year differences contributed similarly and together accounted for 93 - 95% of variation in δD_f values of mallard broods at two Canadian aspen parkland sites. To explore fine-scale processes, we tested whether variation among individual mallards in δD_f was related to temporal patterns of δD_p , precipitation volume, or antecedent climate processes at one site in prairie Canada during 1994-1998. Variation in δD_f was best explained by δD_p values dating from the end of feather synthesis to the beginning of the previous growing-season (i.e., >12 months earlier). High levels of growing-season precipitation resulted in depleted δD_f values during the same year whereas δD_f values were more enriched when precipitation was low; these patterns were consistent with expected patterns in δD_p . The effect of antecedent climate processes was pronounced when the site experienced drought and little snowfall accumulation during the previous winter. Similar to terrestrial and aquatic species examined at large spatial scales, we found support for a relationship between amount-weighted growing-season δD_p and δD_f values during spring-summer for mallards at small spatial scales. Our findings for annual and seasonal shifts in δD_f values help to clarify why individual origin assignments can be confounded for wetland birds at fine spatial scales, at least in areas of complex hydrological coupling in small wetlands of the prairie pothole region. In such cases, annual patterns of δD_p that incorporate contributions from cross-seasonal

precipitation events and the hydrology of small wetlands may refine the stable isotope approach for inferring origins of wetland-associated birds.

A1.2 INTRODUCTION

Strong continental-scale geospatial structure and correlation between hydrogen isotope (D/H) ratios in growing-season precipitation (δD_p) and consumer tissues has improved our understanding of movements and migration in diverse taxa in North America (Cryan et al. 2004, Hobson et al. 2006, Hobson 2008). For terrestrial birds, hydrogen isotope values in feathers (δD_f) have been useful in identifying origins of feather growth at broad spatial scales because of a strong positive linkage between values of δD_p and δD_f (reviewed by Hobson 2008). The resulting continental patterns in consumer tissue δD values have been demonstrated for forest and upland species (Hobson and Wassenaar 1997, Meehan et al. 2004) but less research has been conducted on wetland-associated species (Wassenaar and Hobson 2000, Hebert and Wassenaar 2005a, Hobson et al. 2006, Clark et al. 2006). However, wide-ranging δD_f values of feathers sampled from individuals at the same site (Hobson and Wassenaar 1997, Wunder et al. 2005, Clark et al. 2006, Langin et al. 2007) have been noted. Some of this variation can be due to undetected immigration of individuals to a site (Hobson et al. 2004); however, causes of local variation in δD_f values among individuals using an isotopically homogenous food web are unclear but can be partitioned as measurement error and within- and among-individual differences in δD_f (Wassenaar and Hobson 2006). In addition, variation in timing of feather growth relative to local environmental or food web δD is a factor that has received virtually no attention but which is expected to contribute to variation among individuals with different timing of molt. The δD values in local food webs may fluctuate temporally due to a variety of regional climatic and hydrological processes (e.g., rainfall, evaporation, drought, temperature) that ultimately affect the incorporation of hydrogen into local food webs (Schiegl 1970, Zeigler 1989, Peng et al. 2004, Fig. A1.1). Applications to wetland-associated species in prairie environments are potentially complex to unravel since the δD value of wetlands varying in permanency will depend on historical and hydrological

sources of water δD and temporally dramatic climate variations, such as drought and wet periods.

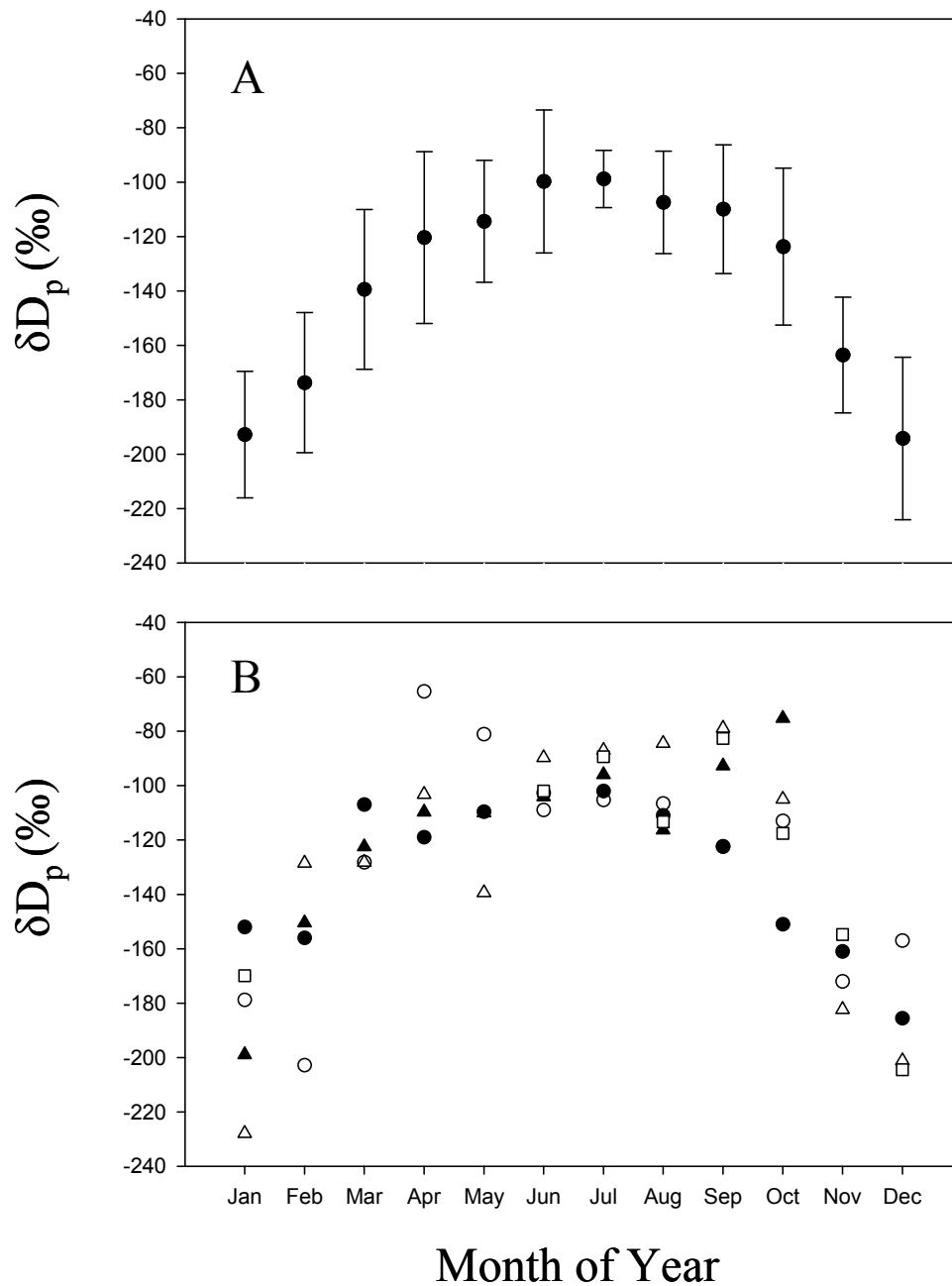


Figure A1.1. Mean (\pm SD) monthly precipitation deuterium values (δD_p) during 1990-2005 (A) and (B) monthly precipitation deuterium values (δD_p) during 1994 (open circle), 1995 (closed circle), 1996 (open triangle), 1997 (closed triangle), and 1998 (open square) at St. Denis Wildlife Area, St. Denis, Saskatchewan, Canada. Months with missing values for 1997 and 1998 indicate that no measurable precipitation (mm) occurred.

Water levels in most prairie wetlands are highly dynamic due to inter-seasonal fluctuations in snowmelt runoff, summer precipitation, and evapotranspiration rates (Murkin et al. 2000). The degree to which δD_f values track fluctuations in water δD associated with these mechanisms will depend upon the rate at which these water hydrogen isotopic fluctuations are ultimately assimilated into local food webs during feather synthesis. The amount of seasonal precipitation is important to food web δD patterns since it determines the hydrogen reservoir available to wetland food webs. For example, during periods of hot drought, wetland and consumer δD values are expected to be comparatively enriched (less negative) to wetter cooler periods (Craig et al. 1963). Alternatively, during periods of higher precipitation, tissue δD values of consumers should be more depleted (more negative) owing to greater inputs of water with depleted δD_p values into wetlands, higher relative humidity, or lower evapotranspiration rates. Alternatively, during years of high snowfall, tissue δD values of consumers may be more depleted owing to a greater influence of snowmelt. An extension of this is that residual water levels in wetlands remaining from a prior wet year may carry over into a drought year, so that isotopic patterns in δD values of consumers may resemble antecedent climate processes.

Waterfowl feathers represent an ideal tissue for testing the predictions mentioned above because feathers of hatching year (HY) birds are grown exclusively from aquatic resources during the growing-season and are metabolically inert after synthesis. Thus, δD_f can be directly compared to environmental sources of δD_p over the same and prior periods to when they are grown. Greater-secondary-covert feather (GSC) synthesis in ducklings is completed in approximately 50 days after hatch (Blais et al. 2001) and female mallards (*Anas platyrhynchos*) retain GSC until after their first breeding-season as yearlings (SY) (Heitmeyer 1989). Thus, feathers grown from natal food webs can be sampled at first breeding locations of SY birds.

Values of δD_f from SY female mallards known to have grown their GSC at a single Canadian prairie site containing numerous wetlands during 1994-1998, were compared to a long-term precipitation record at nearby Saskatoon, Saskatchewan, Canada. Other δD_f values were obtained from SY females which grew GSC at a second Canadian prairie site, and from flightless HY mallards captured for banding at several

widely-separated locations across the Great Plains and northwestern Canada. The first objective was to compare the relative importance of local- versus large-scale effects of space and time to δD_f variation. Then, temporal hypotheses about associations between δD_p and δD_f values for individual feathers grown at the same study area were evaluated. Specifically, I tested whether variation in δD_f was related to δD_p values or precipitation volume during the current growing-season or over periods up to 1.5 years earlier. This study represents the first attempt to assess temporal linkages between δD_p and δD_f values in free-ranging aquatic birds. The motive was to better understand confounding factors than limit assignment of individuals to molt origin using the hydrogen isotope approach.

A1.3 METHODS

Greater-secondary covert feathers (GSC) were sampled from 136 flightless HY mallards captured on wetlands during July-August 1999, 2000, 2001, and 2005 (YEARS) at 11 waterfowl banding stations (SITE) across the mid-continent mallard breeding range (Fig. A1.2). Feathers originated from 2 SITES located in the Northwest Territories ($n = 30$), 1 in northern Saskatchewan ($n = 11$) and 8 in the Canadian prairies (6 Alberta, 1 Saskatchewan, 1 Manitoba; $n = 95$). Most individuals were captured at SITES in traps distributed over $<20 \text{ km}^2$ on large inter-connected wetland complexes or lakes but some individuals in the Canadian prairies were also captured in areas containing smaller wetlands of varying size. Thus, δD_f values reflected the δD values of the SITE food web since feathers from flightless HY could not have been grown elsewhere. SITES were assigned to Canadian boreal forest (BOREAL), boreal transition (BORT), aspen parklands (PARKLAND), and Canadian prairies (PRAIRIE) by comparing their latitude and longitude coordinates to an ecoregion map (Ecological Stratification Working Group 1995).

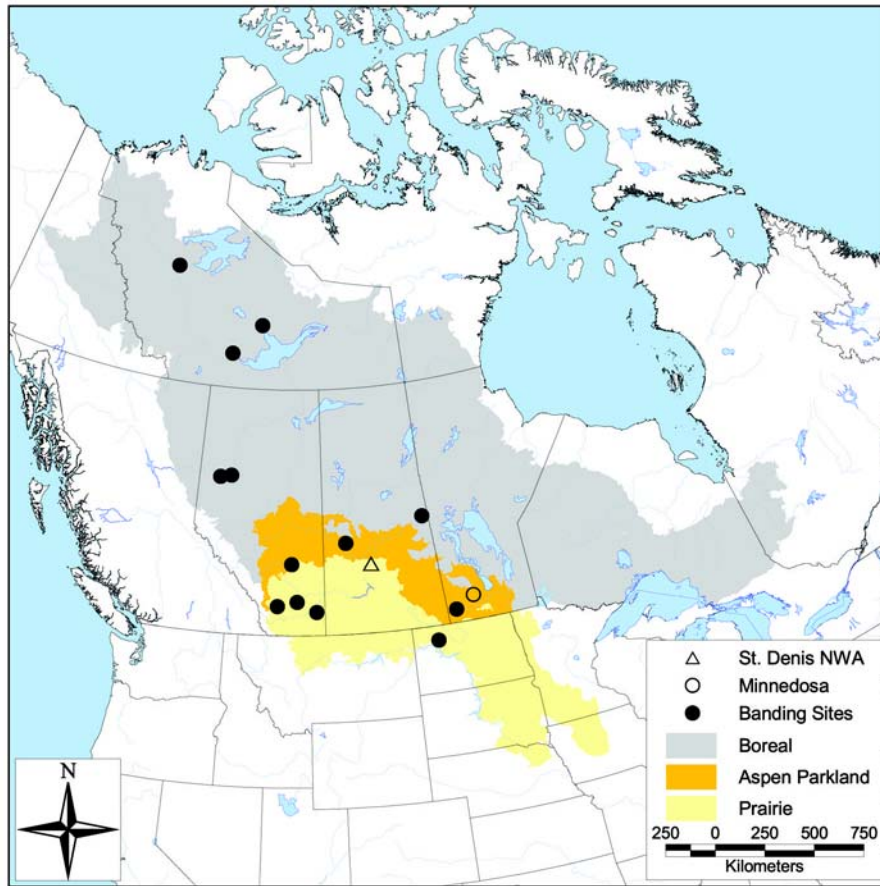


Figure A1.2. Sampling locations of mallard feathers during fall banding (1999-2001, and 2005) and during the breeding-season at St. Denis National Wildlife Area (1994-1998), Saskatchewan and Minnedosa, Manitoba (2002-2005).

Field work was conducted during spring and summer on St. Denis National Wildlife Area (NWA; 385 ha) located near the southern limit of the PARKLAND ecoregion (52°20'N, 106°10'W), approximately 40 km east of Saskatoon, Saskatchewan, Canada. GSC were sampled from 54 mallard females uniquely marked as ducklings in 1994-1998 and recaptured in 1995-1999 as nesting SY. GSC of SY birds would reflect environmental conditions during the prior breeding-season when grown. Of 54 recaptured females, 14 belonged to 7 broods hatched at different times within and among years of the study. Similar activities occurred at a second PARKLAND location near Minnedosa (MB; 1,036ha), Manitoba, Canada, (50°10'N,

99°47'W), during 2002-2005, resulting in GSCs for 15 SY females from 6 different broods. Up to 96 and 377 wetlands of varying permanency were present at NWA (Fig. A1.3) and MB, respectively, during study years when feathers could have been grown. At NWA, routine wetland surveys were conducted during April-July and October each year. In mallards, brood mates typically forage together and use multiple wetlands at least until fledged, so GSC feathers of brood mates should reflect the degree to which δD values of tissues grown at the same time are repeatable, providing feathers were not replaced due to loss elsewhere.

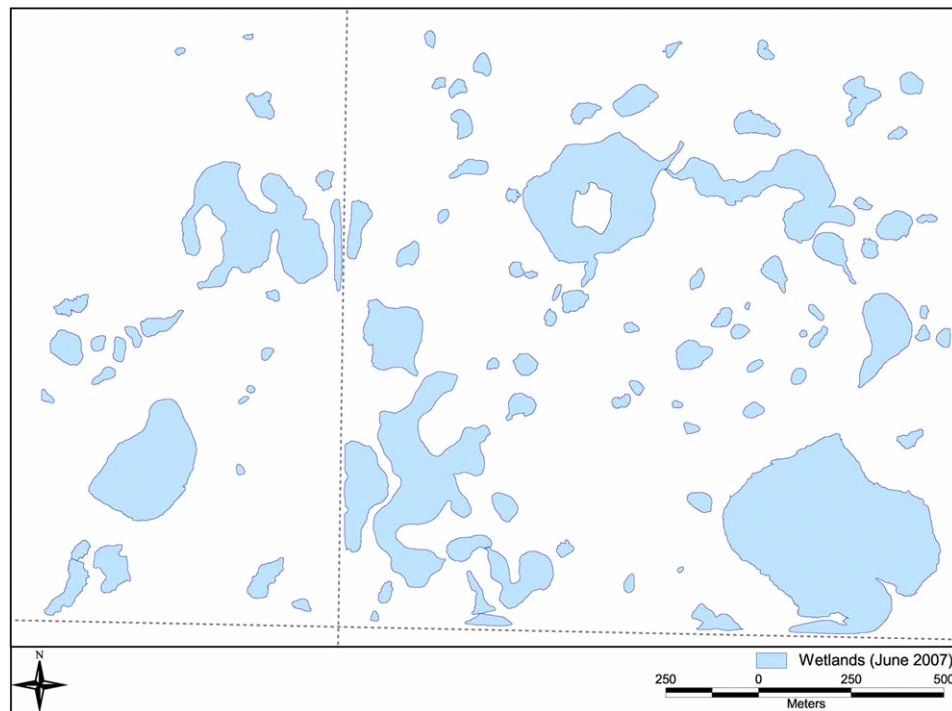


Figure A1.3. Sizes and distribution of wetlands during June, 2007 at St. Denis National Wildlife Area, St. Denis, Saskatchewan, Canada. Growing-season wetland conditions during 2007 were similar to those of 1997 in this study. Dashed lines represent primary grid roads.

Local daily precipitation data were obtained from Environment Canada's Saskatoon Airport weather station, Saskatoon, Saskatchewan, Canada, for 1990-2005, available on the internet (available at: http://www.climate.weatheroffice.ec.gc.ca/Welcome_e.html). These data were used to characterize long-term NWA precipitation patterns and incorporated into time-dependent environmental covariates relative to when GSCs were grown. Small isolated storms occurring at the NWA were probably not represented by Saskatoon data.

Precipitation was sampled monthly for δD analysis at Environment Canada, National Hydrology Research Centre (NHRC), Saskatoon, Saskatchewan, Canada, during 1990-2005, using rain and snow (Nipher) gauges as part of the Global Network of Isotopes in Precipitation (GNIP) program. Feathers were cleansed and processed to determine δD_f values relative to keratin standards as outlined by Wassenaar and Hobson (2003). All δD values are reported in delta notation (δ), in units of per mil (‰), normalized relative to international standards (Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation Scale), and have reproducibility of ± 2.0 ‰. Stable isotope analyses were conducted at Environment Canada, Saskatoon, Saskatchewan, Canada. Nine pairs of recaptured individuals hatched on the same day during the study, so values of δD_f were averaged by hatch day to remove pseudoreplication bias, leaving 45 δD_f values for analyses.

Since prairie wetland water levels may represent an accumulation of past precipitation events, we did not know *a priori* over what length of time accumulated δD_p values in the aquatic food web would be most correlated with values of feathers. We considered four periods of precipitation varying in duration to examine temporal relationships between either the precipitation signal (i.e., δD_p) or volume with δD_f values. These periods included the current growing-season, plus the previous winter, plus the previous growing-season, and plus the second most recent winter where each subsequent period increased in length by six months up to the maximum of ~ 1.5 years possible in our data.

The growing-season was defined by months with mean temperature $> 0^\circ\text{C}$ (Cormie et al. 1994) and so, began on 1 April and ended 30 September and for winter included 1 October – 31 March at Saskatoon. Values of δD_p and cumulative

precipitation volume (CP; mm) were estimated for the current growing-season (D_{cgs} , CP_{cgs} , respectively), through the previous winter (D_{pw} , CP_{pw} , respectively), through the previous growing-season (i.e., beginning one year earlier on 1 April; D_{pgs} , CP_{pgs} , respectively) and through the second most recent winter (D_{2w} , CP_{2w} , respectively) from monthly precipitation data. These indices were then scaled relative to when feather synthesis likely ended (50 days post-hatch) during the current growing-season for each δD_f value. For example, feather synthesis ending on 15 September would have resulted in 168 days (i.e., 1 April – 15 September) of exposure to current growing-season monthly δD_p and CP values. This approach was possible because the exact hatch date of individuals was known. Values representing longer periods were then amount precipitation weighted after accounting for current growing season exposure of individuals. Finally, we used the number of wetlands at hatch (POND) within NWA as an index of residual water inputs due to antecedent climate conditions. Counts of wetlands from NWA surveys were assigned to individuals by pairing the chronology of surveys to hatch date. We assumed that POND values were consistent with wetland trends since surveys were repeated at least monthly from April to July and again in October. Missing monthly precipitation δD and CP values during summer 1993 prevented the estimation of precipitation period covariates >1.5 years and for 1994 δD_f values so these data were excluded from analysis.

Mixed model analysis of variance (ANOVA) was used to assess the relative contributions of banding location (SITE) and time (YEAR) and their interaction to variability in δD_f values in BAND data (SAS Institute, 2008). This was completed by treating SITE as a fixed effect and YEAR and the interaction term as random effects. Candidate models containing different combinations of these effects were allowed to compete for support by the data using an information theoretic approach (Burnham and Anderson 1998). Models were considered well supported if the difference of their Akaike's Information Criterion score (ΔAIC) was <2.0 units relative to the model with the minimum score (Burnham and Anderson 1998). At NWA and MB sites, a hierarchical model was also used to assess variance components of δD_f for annual differences among broods and within-year differences among broods treating YEAR as a fixed effect.

Annual variability of δD_f and δD_p values at NWA was evaluated using ANOVA. Pooled analysis of general linear models was used to partition variance in δD_f due to additive effects of δD_p and CP and for POND. Interaction terms for δD_p and CP period covariates were only considered for those covering the same time period (e.g., δD_{cgs} and CP_{cgs}). We applied an information theoretic approach to evaluate the relative support for candidate models (Burnham and Anderson 1998). The sum of normalized Akaike weights (w_i) was interpreted as a measure of precipitation period and covariate importance in the context of the set of candidate models (Burnham and Anderson 1998). All statistical analyses were performed using the GLM procedure in SAS (version 9.1, SAS Institute, Cary, North Carolina).

A1.4 RESULTS

A1.4.1 *Variance components at broad and local scales*

Model selection results indicated that most parsimonious model included effects for SITE, YEAR, and SITE-YEAR interaction (Table A1.1). The rest of candidate models were not well supported by the data. Variance components for the random effects of YEAR and SITE-YEAR interaction were 0% and 32%, respectively. Within ecoregions, the relative contributions of random effects due to YEAR and SITE-YEAR interaction differed in each ecoregion (Table A1.2). Fine-scale assessment of brood data at NWA and MB indicated that annual δD_f differences were significant (nested ANOVA_{NWA}, $F_{2,4} = 21.08$, $P < 0.001$ and nested ANOVA_{MB}, $F_{2,3} = 34.32$, $P < 0.001$, respectively). Variance components for differences among broods within years were 93% at both NWA and MB, whereas within brood variation was low (7% and 5%, respectively).

Table A1.1. Model selection results examining variation of δD_f values (‰) relative to sampling location (SITE), year of sampling (YEAR) from mixed model analysis. Model parameter constraints included additive (+) and interaction (*). Shown for each model are Akaike's Information Criterion adjusted for small sample size (AIC_c), relative AIC_c difference (ΔAIC_c), number of parameters (K), model likelihood (L_i), and model weight (w_i).

Model	AIC_c	ΔAIC_c	K	L_i	w_i
SITE + YEAR + SITE*YEAR	338.9	0.00	49	1.00	1.00
SITE	393.5	54.6	15	0.00	0.00
SITE + YEAR	402.5	63.6	19	0.00	0.00
YEAR	415.9	77.0	6	0.00	0.00

Table A1.2. Variance component estimates (%) from analysis of variance for the random effects of year (YEAR) and fall banding station-YEAR interaction (INT) of variation in δD_f values from flightless mallards sampled within boreal forest (BOREAL), boreal transition (BORT), aspen parkland (PARKLAND), and prairie (PRAIRIE) Canada, 1999-2001 and 2005.

Effect	Ecoregion			
	BOREAL	PEACE	PARKLAND	PRAIRIE
YEAR	<0.1	29.6	45.2	11.3
INT	57.1	5.6	0.0	0.0
ERROR	42.4	64.7	54.8	88.7

A1.4.2 *Temporal patterns at a parkland site*

The δD_f values of SY mallard females recaptured at NWA varied annually (ANOVA, $F_{4,40} = 27.5$, $P < 0.01$, Figure 4) while δD_p values did not (ANOVA, $F_{4,23} = 0.76$, $P = 0.56$) (Table A1.3). Variation in δD_f was best modelled to include the effect of δD_{pgs} (Table A1.4). This model received approximately twice as much support, based on AIC_c weight (w_i), than the next best model which included the effects of δD_{pw} and CP_{pw} . Models which accounted for precipitation values during the previous growing-season received 58% of cumulative normalized w_i , relative to those of current growing-season (6%), through the previous winter (24%), through second most recent winter (12%), and POND (<1%). The covariate δD_{pgs} occurred in 2 of 3 top-ranked models, CP_{pgs} occurred twice in the top 4, and δD_{pw} and CP_{pw} were the only other covariates to appear in the 5 top-ranked models. POND was not well supported relative to other models (Table A1.4).

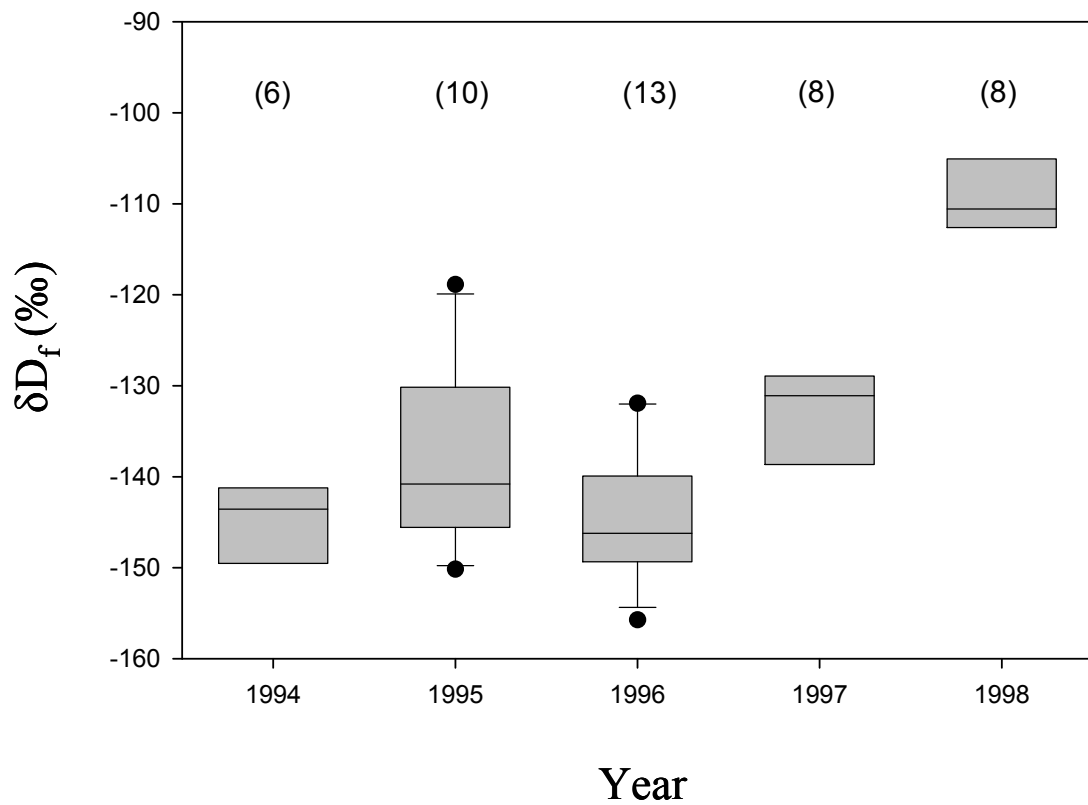


Figure A1.4. Annual distributions of deuterium values from yearling mallard female feathers (δD_f) grown at St. Denis Wildlife Area, St. Denis, Saskatchewan, Canada during 1994-1998. Shown are median (horizontal line within shaded box), 25th percentile (box boundary nearest zero), 75th percentile (box boundary farthest from 0), the 10th and 90th percentiles (horizontal lines), and extreme values (closed circles). Sample sizes are in parentheses.

Table A1.3. Mean ponds at hatch (Ponds), cumulative precipitation volume (mm) during winter prior to hatch (CP_{wint}) and current growing-season (CP_{cgs}), and deuterium values (‰) in amount-weighted growing-season rainfall (δD_p) and yearling mallard feathers (δD_f) during 1994-1998 at St. Denis National Wildlife Area, Saskatchewan, Canada. Mean estimates, standard deviations and sample sizes (SD, n), are shown for Ponds, δD_p , and δD_f and point estimates for CP_{wint} and CP_{cgs} .

Year	Variable				
	Ponds (SD, n)	CP_{wint}	CP_{cgs}	δD_p (SD, n)	δD_f (SD, n)
1994	73 (13.5, 6)	66.9	285.0	-95.3 (13.7, 6)	-145.4 (6.0, 6)
1995	41 (4.0, 10)	77.2	247.8	-108.0 (6.0, 6)	-138.8 (9.6, 10)
1996	78 (5.0, 13)	77.3	362.4	-96.6 (19.6, 6)	-144.7 (7.4, 13)
1997	83 (13.1, 8)	79.3	244.1	-104.7 (8.6, 6)	-133.9 (7.3, 8)
1998	33 (0.7, 7)	12.5	170.8	-99.1 (10.4, 4)	-110.5 (4.9, 7)

Table A1.4. Top five candidate models evaluating sources variation in yearling mallard feather deuterium values at St. Denis Wildlife Area, St. Denis, Saskatchewan, Canada, during 1995-1998. Effects considered included estimates of amount-weighted growing-season precipitation deuterium and cumulative precipitation volume during the current growing-season (D_{cgs} , CP_{cgs} , respectively), through the previous winter (D_{pw} , CP_{pw} , respectively), the previous growing-season (D_{pgs} , CP_{pgs} , respectively) and the second most recent winter (D_{2w} , CP_{2w} , respectively). Also shown is the least supported candidate model; D_{cgs} . Model parameter constraints included additive (+) and interaction (*). Shown for each model are Akaike's Information Criterion adjusted for small sample size (AIC_c), relative AIC_c difference (ΔAIC_c), number of parameters (K), model likelihood (L_i), and model weight (w_i).

Model	AIC_c	ΔAIC_c	K	L_i	w_i
D_{pgs}	78.47	0.00	3	1.00	0.31
$D_{pw} + CP_{pw}$	79.84	1.37	4	0.50	0.16
$D_{pgs} + CP_{pgs}$	80.84	2.37	4	0.31	0.09
CP_{pgs}	81.00	2.53	3	0.28	0.09
$D_{pgs} + CP_{pgs} + D_{pgs} * CP_{pgs}$	81.09	2.62	5	0.27	0.08
D_{cgs}	94.01	15.54	3	0.00	0.00

A1.5 DISCUSSION

The practice of using tissue deuterium values to assign individuals to regional origins is possible because of predictable broad spatial patterns in long-term values of growing-season precipitation (Bowen et al. 2005) and local consumer tissues (Hobson 2005). Our finding that spatial components, in particular latitude, were an important source of variability in δD_f values at broad regional scales across northcentral North America is consistent with other reports (Hobson and Wassenaar 1997, Meehan et al. 2004, Clark et al. 2006). However, spatial aspects were less important to δD_f variability within ecoregions (Table A1.2) and several factors could have contributed to this pattern. In boreal forest, all sampling locations were situated on or adjacent to river systems and aquatic food web values at these sites are likely influenced by water δD values from tributaries spanning a much broader area. Local precipitation dynamics affecting the contribution of tributaries to river δD values may explain the importance of the interaction between site and year for boreal forest and this aspect warrants further investigation. Within boreal transition, aspen parkland, and prairie, there was little latitudinal separation among sites, so the observation that spatial variation was not important within these regions is not surprising (Table A1.5).

Table A1.5. Annual mean (SD, n) δD_f values (‰) from flightless mallards captured at fall banding stations in the boreal forest (BOREAL), boreal transition (BORT), aspen parklands, (PARKLAND), and prairies (PRAIRIE) of western Canada. Also shown are site latitude (LAT, ° N) and longitude (LONG, ° W) and political location (LOC).

Ecoregion	LOC	LAT	LONG	Year			
				1999	2000	2001	2005
BOREAL	SK	54.0	-102.3	-187.6, 55.0 (6)	-	-166.6, 8.2 (5)	-
BOREAL	NT	61.5	-118.3	-181.0, 44.3 (5)	-	-182.6, 3.4 (5)	-148.7, 24.3 (5)
BOREAL	NT	62.8	-115.5	-158.2, 7.5 (6)	-	-159.9, 3.5 (4)	-167.0, 3.2 (4)
BOREAL	NT	65.0	-125.0	-188.3, 5.7 (3)		-180.3, 2.4 (4)	
BORT	AB	56.0	-118.3	-161.8, 55.4 (4)	-165.3, 14.8 (6)	-157.9, 9.9 (5)	-174.5, 7.1 (6)
BORT	AB	56.1	-117.4	-148.7, 15.2 (4)	-157.7, 14.6 (7)	-	-
PARKLAND	MB	49.6	-100.8	-	-	-121.8, 12.6 (4)	-124.4, 8.0 (6)
PARKLAND	AB	52.2	-112.4	-152.8, 17.8 (5)	-	-	-136.5, 26.5 (6)
PARKLAND	SK	53.1	-108.3	-164.0, 12.5 (6)	-	-129.6, 3.3 (5)	-
PRAIRIE	ND	48.3	-102.3			-115.6, 1.9 (5)	-99.1, 34.4 (6)
PRAIRIE	AB	50.1	-110.6	-128.9, 6.9 (4)	-	-	-137.4, 21.5 (6)
PRAIRIE	AB	50.3	-113.4	-135.2, 27.0 (5)	-	-143.2, 4.9 (5)	-
PRAIRIE	AB	50.5	-112.0	-145, 16.7 (6)	-	-164.1, 7.3 (5)	-

I expected temporal components to be important in boreal transition, aspen parkland, and prairie sites because precipitation is an important and temporally dynamic source of water in pothole wetlands which waterfowl use in these ecoregions (Murkin et al. 2000). For this same reason, I expected temporal effects to be less pronounced than spatial effects in boreal forest because permanent water bodies, such as lakes, are less reliant on precipitation as a source of water (Mitsch and Gosselink 2000). I also expected reduced evapotranspiration rates in boreal forest's relatively colder climate to result in greater repeatability of banding sampling locations δD_f values versus more southern regions. The results indicate that annual variability accounted for 0–45% of variation in δD_f but was less important relative to variation among individuals at sites (i.e., error term) within ecoregions (Table A1.2). Residual error accounted for 42–89% of variance and was the primary source of δD_f variability within ecoregions. This pattern could arise if individuals were sampled from different wetlands within and among years at sites or if significant spatiotemporal variation in food web deuterium values occurs within large wetland complexes or lakes targeted by waterfowl banders. If either of these occurred in samples then contributions due to year may be biased low and residual error biased high. Alternatively, the role of annual differences in precipitation and seasonal evapotranspiration may have been less than I expected. In lieu of these potentially confounding factors, the results of this study highlight that processes occurring at fine spatial scales are a major source of δD_f variability.

Fine-scale assessments of brood δD_f values at St. Denis and Minnedosa supported the hypothesis that year effects are important sources of δD_f variance in samples but indicated that most variance within years is related to differences in hatching dates and wetland use by brood-rearing females. Comparison of water δD values sampled from a semi-permanent (mean = -112.6, SD = 17.4, n = 5) and a permanent (mean = -84.4, SD = 30.7, n = 5) wetland during the same five months at NWA indicated their signals were unique (paired t-test, $t_4 = 4.22$, $P = 0.01$) (G. van der Kamp, National Water Research Institute, Saskatoon, unpubl. data). Thus, wetland conditions presumably contributed to variation in δD_f as well because females raised broods on many different wetlands (Gendron and Clark 2002).

A1.5.1 Sources of temporal variation at a single site

The results of this study demonstrate that annual variation in δD_f of consumers is related to dynamics of environmental sources of water in wetlands used by ducks. Langin et al. (2007) showed in American Redstart (*Setophaga ruticilla*) nestlings, a terrestrial songbird, that δD_f values grown at the same location varied annually whereas those of adults did not; whether these patterns were related to among-year shifts in isotopic composition of dietary items was not determined. The results of this study imply that predicted values would vary annually in both adults and nestlings relative to environmental sources food web δD values but inconsistencies may reflect differences between aquatic and terrestrial food webs. On the other hand, the site used by Langin et al. (2007) was essentially riparian and differences could have been due to differential access to aquatic emergent insects within and between years.

As with other studies, I found a positive relationship between δD_p and δD_f values (Hobson and Wassenaar 1997, Meehan et al. 2004) but that this relationship for yearling mallards at St. Denis is best described as a function of cross-seasonal accumulation of precipitation δD signals. My results indicate that an average of δD_p dating back to the prior growing-season best approximated annual patterns of δD_f (Table A1.4, Fig. A1.5). I recognize that mallard ducklings are unlikely assimilating deuterium into growing tissues directly by consuming precipitation so, I expect that this term represents the period over which current water levels in wetlands have accumulated from past precipitation and evapotranspiration. While summer rainfall is not usually the primary source of water in prairie wetlands (Woo and Roswell 1993, Murkin et al. 2000), it could produce higher relative humidity and slow the enrichment of wetland δD values from summer evapotranspiration relative to when the local climate is drier. This process is apparent in my data when comparing annual fluctuation between growing-season precipitation volume and δD_f values (Table A1.3).

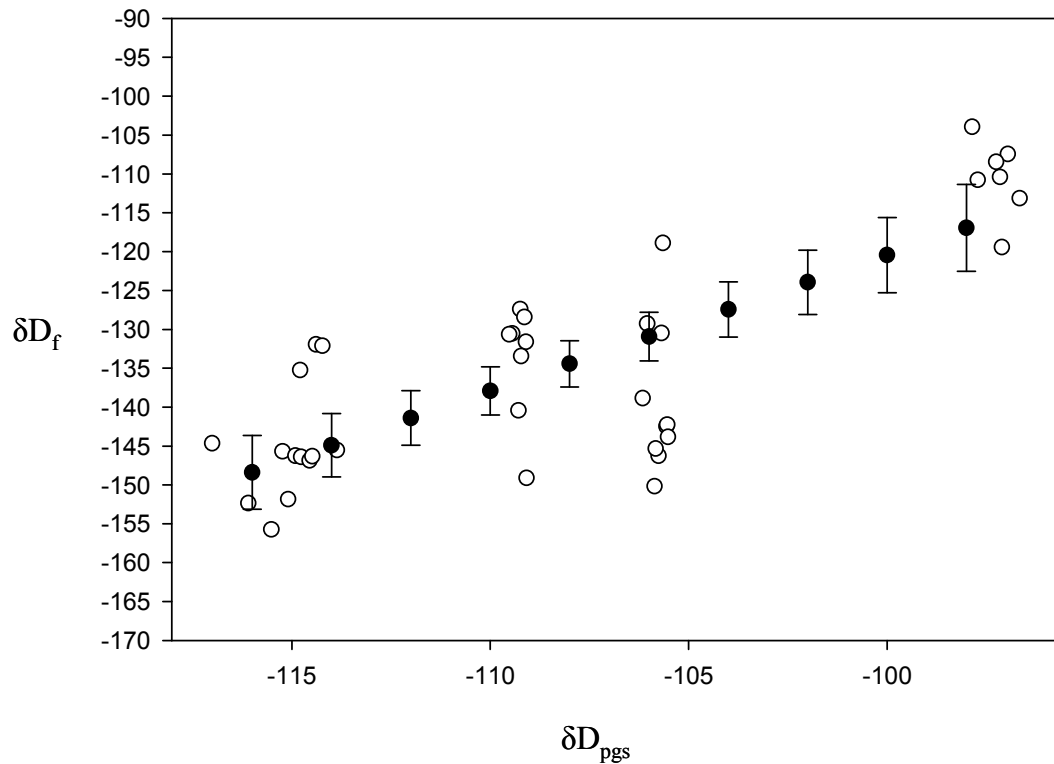


Figure A1.5. Expected mean ($\pm 95\%$ CI) deuterium values (‰) of feathers (δD_f , closed circles) versus amount-weighted precipitation for a period extending from the *prior* growing-season (i.e., about 15 months earlier) through the end of feather synthesis (δD_{pgs}) for yearling female mallards at St. Denis National Wildlife Area, Saskatchewan, Canada, during 1995-1998. Also shown are plots of individual δD_f (open circles) and δD_{pgs} values.

There was some model support for the importance of precipitation occurring during the previous winter (Table A1.4). At St. Denis, 12.5 mm of winter precipitation occurred prior to spring 1998, compared to ~70 mm during other years (Table A1.3). The lower amount of snowfall during the 1997-98 winter resulted in drier spring wetland conditions and values of δD_f which were more enriched than in previous wetter years (Table A1.3, Fig. A1.4). Winter month δD_p values are generally much more depleted than months during the growing-season (Fig. A1.1). In the absence of winter precipitation, δD values of the wetland food web at spring thaw should resemble those

of the prior fall because values do not change in ice (Dansgaard et al. 1960). Large shifts in δD_f values during transitional states of prairie wet-dry cycles may occur because the frequency of precipitation events is more dynamic at wet-dry transitions than within wet or dry periods (see Peng et al. 2004). Saskatoon precipitation data for 1990-2005 showed that little or no snowfall preceded the beginning of drought conditions at St. Denis. While the volume of precipitation from snow can be low relative to that of rain during the growing-season, snowmelt from basin catchments is the primary hydrological source of high water levels in St. Denis wetlands (Woo and Rowsell 1993, van der Kamp and Hayashi, *in press*).

Models which described the relationships between δD_f and current growing-season precipitation values were not well supported relative to longer periods of accumulation (Table A1.4). Values of δD_p did not vary significantly among the years during the study and fluctuated annually between relative depletion and enrichment (Table A1.3). While δD_f values also fluctuated annually, they did not mimic the trend of δD_p values. As a result of these inconsistencies, annual estimates of current growing-season δD_p did not provide reliable predictions of annual δD_f values (Fig. A1.6). However, δD_f values might be expected to resemble more recent precipitation values when wetlands are suddenly inundated with water following the end of drought.

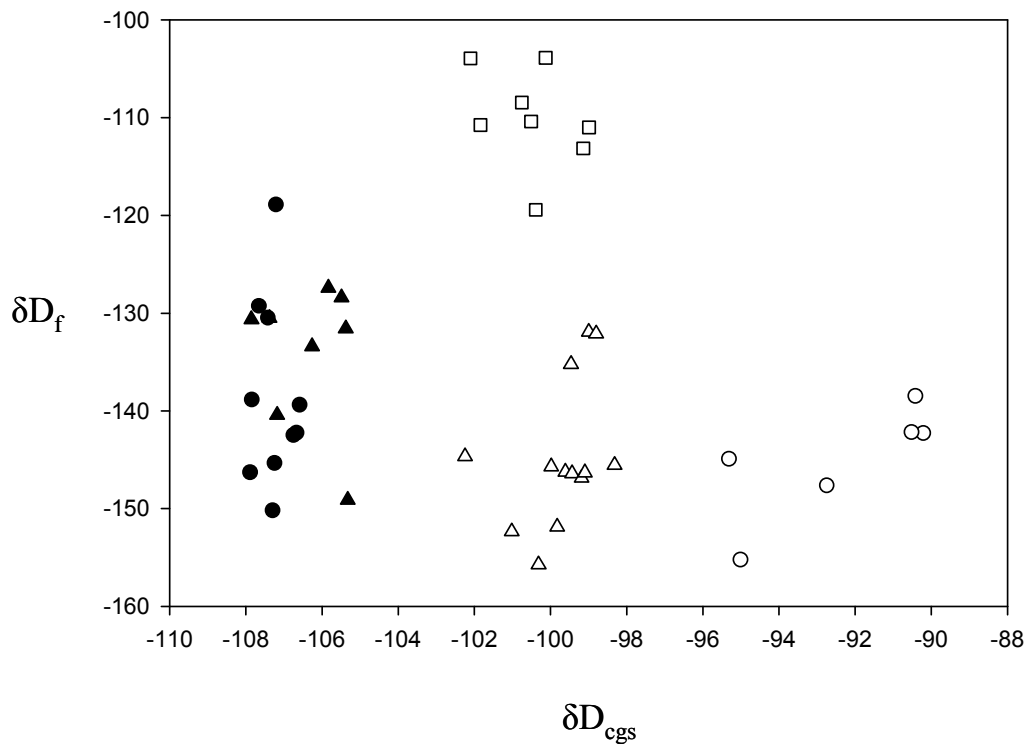


Figure A1.6. Annual values of deuterium in feathers (D_f) and current growing-season precipitation (D_{cgs}) of female mallards at St. Denis National Wildlife Area, Saskatchewan, Canada, during 1994 (open circle), 1995 (closed circle), 1996 (open triangle), 1997 (closed triangle), and 1998 (open square).

The relative contribution of temporal variation in δD_f occurring at wetland sites can be similar to spatial variation in some North American mid-continent breeding-regions. Fine-scale values of δD_f in mallards were most closely associated with cross-seasonal δD_p values dating back to the prior growing-season. In particular, winter precipitation may be an important determinant of δD_f values in small prairie wetlands because snowmelt runoff in the spring is the most influential source of wetland recharge (Woo and Rowsell 1993). I found little evidence supporting that growing-season pattern of δD_p immediately preceding and during feather synthesis influenced δD_f values. Variation in St. Denis δD_f values reflected how wetlands were regulated by cross-seasonal changes in δD_p . While this study focussed on variation in δD values of

consumer tissues in aquatic systems, similar relationships between climate, food web, and consumers may also apply to δD values in terrestrial systems where local productivity can be driven by spring snowmelt.

Values of δD_f have been used to assign origin of migratory birds (Hobson and Wassenaar 1997, Hebert and Wassenaar 2005a) and to trace individual movements, dispersal, and population connectivity (Webster et al. 2002, Hobson 2005, 2008). These applications are based on the assumption that the GNIP database adequately reflects site-specific food web δD values in any given year. There are studies for which this assumption appears valid (Clark et al. 2006, Langin et al. 2007) and others, less so (Meehan et al. 2003, Lott and Smith 2006). Most practitioners of the isotope approach to inferring origins recognize this source of uncertainty (Hobson 2005, 2008). Origin assignment models developed from known-source δD_f values are most reliable at broad versus fine spatial scales (Hebert and Wassenaar 2005a, Wunder et al. 2005, Syzmanski et al. 2007). Variability in site-specific precipitation patterns over 1-2 years may explain why the spatial resolution of δD_f origin assignment is limited to broad spatial scales in northcentral North America, especially for waterfowl. For areas with low among-year variance, tissue values of consumers may better match those expected from δD_p basemaps (e.g., Langin et al. 2007). In the case of St. Denis, there would have been little success in predicting individuals to have originated specifically from St. Denis because δD_f values tracked changes in the local environment that also resembled the range of values at other distant locations within the aspen parklands or other ecoregions. This problem is diminished at broader spatial scales as variation due to local effects is reduced compared to continental patterns in δD_p (Craig et al. 1963, Rozanski et al. 1992). Clearly, the magnitude of variation in δD_p and δD_f at any given site from those predicted from isotopic basemaps will depend on deviations from climate norms, local hydrology, and error in measures of δD (Wunder and Norris 2008). Only when these and other sources of variation are known for a given application will it be possible to evaluate how well the use of feather δD values can be used to infer origins of individuals at fine spatial.